2020-06

Nutrient hotspots for wild grazing ungulates in a miombo ecosystem, western Tanzania

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NUTRIENT HOTSPOTS FOR WILD GRAZING UNGULATES IN A MIOMBO ECOSYSTEM, WESTERN TANZANIA

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A dissertation Submitted in Partial Fulfillment of the Requirements for the Degree of Doctor of Philosophy in Life Science and Engineering of the Nelson Mandela African Institution of Science and Technology

Arusha, Tanzania

June, 2020

ABSTRACT

While the movement pattern of grazing ungulates is strongly dependent on forage quality whose use of nutrient hotspots has rarely been quantified, especially in miombo ecosystems where soil-nutrient quality is low. Few experiments have been conducted to determine the role of nutrient hotspots derived soils in improving forage quality in miombo ecosystems. Nutrient hotspots strongly attract ungulates in nutrient poor habitats such as savanna systems. However, little is known about their seasonal importance for different grazing ungulate species. No study has quantified the potential re-distribution of nutrients into the surroundings away from hotspots. The current study assessed nutrient hotspot (i.e., grazing lawns and termite mounds) use by ungulates in a highly threatened miombo ecosystem of the Issa valley, western Tanzania. Study used indirect observation, camera traps and stable isotope analyses over a one year period to identify seasonal and spatial variations in habitat use of various wild mammalian grazers around ten termite (*Macrotermes* sp.) mounds, six grazing lawns and their respective control sites. Grazer visitation rates were nine and three times higher on termite mounds and grazing lawns, respectively compared to control sites. During the rainy season, termite mounds were more frequently used than grazing lawns while grazing lawns were more frequently used during the dry season. A total of 32 camera stations recorded 244 wildlife encounter events in total. Camera data show that ungulates used hotspot areas four times more frequently in comparison to their control plots. *Cynodon dactylon* grass planted in soils derived from termite mounds had twice as high nitrogen and phosphorous contents compared to grasses planted in grazing lawn soils and control site soils. Stable isotope analysis highlighted that dung deposited by grazers around hotspots originated from grasses within hotspot areas, hence proving that grazers are responsible for modifying nutrient stability around these hotspots. This study results highlight that nutrient hotspots play a significant role in influencing seasonal soil and forage nutrient dynamics, habitat selectivity, and hence grazing activities/ movements of wild ungulate grazers in miombo ecosystems. The study concludes that nutrient hotspots are important for various ungulates in otherwise nutrient – poor miombo systems.

Key words: Dung, Grazing lawns, Stable isotopes, Termite mounds, Issa valley

DECLARATION

I, Gabriel Mayengo do hereby declare to the Senate of the Nelson Mandela African Institution of Science and Technology that this dissertation is my own original work and that it has neither been submitted nor being concurrently submitted for degree award at any other institution.

Gabriel Mayengo

Name of the candidate	**Signature**	**Date**

The above declaration is confirmed

Prof. Anna C. Treydte

Supervisor 1	**Signature**	**Date**

Dr. Alex K. Piel

Supervisor 2	**Signature**	**Date**

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CERTIFICATION

The undersigned certify that have read and hereby accept the dissertation titled "Nutrient Hotspots for Wild Grazing Ungulates in a Miombo Ecosystem, Western Tanzania", is written by Gabriel Mayengo under supervision of Prof. Anna C. Treydte and Dr. Alex K. Piel at the NM-AIST. I approve the dissertation for submission to the NM-AIST senate for award of the PhD degree in Life Science and Engineering (Biodiversity Conservation and Ecosystems Management).

Prof. Anna C. Treydte

Supervisor 1	**Signature**	**Date**

Dr. Alex K. Piel

Supervisor 2	**Signature**	**Date**

ACKNOWLEDGEMENTS

First and foremost, I am eternally thankful to the Almighty God for giving me the strength and courage I needed throughout completion of this doctoral program.

My sincere thanks and appreciation to my supervisors Professor Anna C. Treydte and Doctor Alex K. Piel for their guidance, support, patience and friendship that ensured the successful implementation of the research and preparation of this dissertation work.

Part of the work presented in this dissertation was carried out in Hohenheim University together with Hamburg University of Applied Sciences in Germany. I would like to thank Dr. Wolfgang Armbruster from Hohenheim University, Professor Thomas Clemen from Hamburg University of Applied Sciences for allowing me to work in their laboratories and for their valuable advice and guidance to complete my research work, analyze the data and the writing of this document. I also thank Ulfia Lenfers for her technical guidance. I would like to extend my thanks to Laboratory technicians at Hohenheim University and Sokoine University of Agriculture for their assistance during sample preparations and their technical support.

I am grateful to Allen Nyang'anyi, David Maleko and Festo Luanda from Sokoine University for their support in grass identification during the course of my studies, Emmanuel Mboya from National Herbarium for his assistance during grass identification as well, also all the field assistants at (GMERC) Project, Jonas Bukende, Mlela Juma, Alkado Hassan, Patrick Hassan, Simon Hassan, Mariana Marco, Milka Nyamubi, Hussein Juma, Theresia Michael, Baba Doa and Baruani Juma for their constant support in collecting data samples. Much appreciation to my friends Dr. Never Zekeya, Dr. Fortunatus Jacob, Dr. Anibariki Ngonyoka, Dr. Naza Mbaga, Dr. Issakwisa Ngondya, Dr. Munguatosha Ngomuo, Dr. Nicholous Mnyambwa, Dr. Okumu Ochanga, Ayoub Assenga, Aidan Telesphory, Ibrahim Fanuel, Fidelcastrol Kimario, Rudolf Mremi, Prof. Japhari Kideghesho as well as staff and students at the College of African Wildlife Management, Mweka.

My sincere appreciation and love to my lovely wife Edna Brown Angetile Mwamalala, my daughter Gabriella, and my son Gabrielson for their love and support, which gave me enough strength to successfully complete this program. I also would like to thank my parents Mr. Maurice Mayengo Kanegene and Elizabeth Samson Senkwale, father in-law Gideon Brown

Angetile Mwamalala and my mother in-law Paulina Stephen, other family members including my brothers John, Emmanuel and Peter, my sisters Beatrice and Juliana, in-laws John, Moses and Joseph and all family members for their moral support and encouragement.

I am also indebted to thank my friends we studied together at Katubuka Primary School, Mwembeni Primary School, Mazengo Technical Secondary School, St John's University, The University of Dodoma and The Nelson Mandela African Institution of Science and Technology. Further, I extend my appreciation to staff and students at Msalato Girls Secondary School, Salesian Seminary and Mineral Resources Institute where I have worked before joining my PhD studies.

Also my sincere regards to all people and organizations I interacted with during the course of my PhD studies. In one way or another you assisted me in accomplishments of this work. Without their assistance, this dissertation would not be possible.

This research was partially funded by The German Academic Exchange Service (DAAD), the African Centre for Research, Agricultural advancement, Teaching Excellence and Sustainability (CREATES), and the Greater Mahale Ecosystem Research and Conservation Project (GMERC). Further, I would like to acknowledge the loan support I received from Higher Education Student's Loans Board (HESLB). All funders gave me an opportunity to start a doctoral program and pursue my dream of becoming a scientist through an internationally highly reputable University, The Nelson Mandela African Institution of Science and Technology.

DEDICATION

This work is dedicated to my lovely wife Edna Brown Angetile Mwamalala and to my parents Maurice Mayengo Kanegene and Elizabeth Samson Senkwale.

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LIST OF ABBREVIATIONS AND SYMBOLS

BEF	Before Setting Experimental Plots
CLIP	Clipped Plots
CONT	Controls
COSTECH	Tanzanian Commission for Science and Technology
FERT	Fertilized Plots
GL	Grazing Lawns
GLMM	Generalized Linear Mixed Model
ICP-OES	Inductively Coupled Plasma - Optical Emission Spectrometer
IRMS	Isotope Ratio Mass Spectrometry
NGL	Non-grazing Lawns
NTM	Non-termite Mounds
TAWIRI	Tanzania Wildlife Research Institute
TM	Termite Mound

CHAPTER ONE

INTRODUCTION

1.1 Background of the problem

Ungulates are hoofed mammals forming rich assemblages of grazing and browsing animal groups inhabiting African ecosystems (Treydte *et al*., 2006). Once of these ecosystems are miombo woodlands, which is a vegetation type that is highly found western Tanzania (Iida *et al*., 2012; Kavana & Kakengi, 2014). The distinguished plants and animals found in the miombo woodland are thought to originate from both the tropical rainforest and the savanna ecosystems (Iida *et al*., 2012). However, recently miombo forests in eastern Africa have been threatened by human activities such as slash-and-burn farming and deforestation (Iida *et al*., 2012). Groups of ungulates inhabit miombo ecosystems (Caro, 2008; Iida *et al*., 2012; Mayengo *et al*., 2020; Piel *et al*., 2019) need high quality forages to maintain and promote their reproduction potential (Frank *et al*., 1998). Furthermore, aerial censuses carried out between 1988 and 2002 show that populations of different large wild ungulate species in miombo ecosystems have declined, with anthropogenic activities being responsible for changes in this important ecosystem (Caro, 2008).

"Nutrient hotspots" (Shantz *et al*., 2015) i.e., areas around termite mounds and on grazing lawns, show higher plant productivity (Poorter & Jong, 1999), nutrient contents (Jouquet *et al*., 2016; Treydte *et al*., 2011) abundance and diversity (Hutson, 1979) compared to areas further away from them. Particularly in nutrient-poor systems such as miombo woodlands ecosystem (Van der Waal *et al*., 2011) these hotspots are thus, important for maintaining ungulate populations. Chemical properties of soil have been reported to differ significantly around termite mounds and grazing lawns (Dangerfield *et al*., 1998) compared to surrounding areas. Grasses with high nutrients and freshly re-grown were found to be important cues attracting ungulates in savanna systems (Treydte *et al*., 2010). Furthermore, ungulates in savanna ecosystems were found to concentrate their nutrients as a result of foraging closer to the nutrient hotspots compared to their controls (Treydte *et al*., 2006), contributing to a long term grazing lawn effect of the landscape.

As described elsewhere, ungulates select areas with quality forage (Cromsigt & Olff, 2008; Mayengo *et al*., 2020; Treydte *et al*., 2011), that show no predation (Kuijper *et al*., 2014).

Hence, their distribution is highly regulated by predation risks (Theuerkauf & Rouys, 2008). In selecting areas with no predation, animals use various cues like predator scat, olfactory cues, sight and habitat visibility (Kuijper *et al*., 2014). Areas around grazing lawns are highly preferred by ungulates because they are flat, and predators or any danger can easily be seen from a distance (Hempson *et al*., 2015) providing a high degree of security to ungulates. Furthermore, areas around termite mounds are used by ungulates to scan the environment for possible predators (Mayengo *et al*., 2020). Groups of ungulates in various ecosystems tend to develop unique combination of body size, gut morphology, social structure (solitary or gregarious) and foraging strategy (grazer, browser and mixed-feeder) (Schuette *et al*., 2016).

Clearly, among the challenges for conservation programs in African protected areas is an accurate assessment of populations of larger mammals (Waltert *et al*., 2008) and their diet preferences, which is crucial both for monitoring success of existing management actions and for formulating future management options (Caro, 2008; Waltert *et al*., 2008). Currently, Tanzania is facing increasing wildlife conservation challenges, such as encroachment into protected areas, loss of wildlife habitats and illegal resource harvest (TAWIRI, 2015). All these challenges together have resulted in wildlife population declines. However, few ecological and behavioral studies of mammals other than chimpanzees have been conducted in miombo ecosystems (Iida *et al*., 2012). Hence, more scientific information is needed in less studied areas like in western Tanzania on how to improve conservation efforts of various natural resources found in this ecosystem (TAWIRI, 2015).

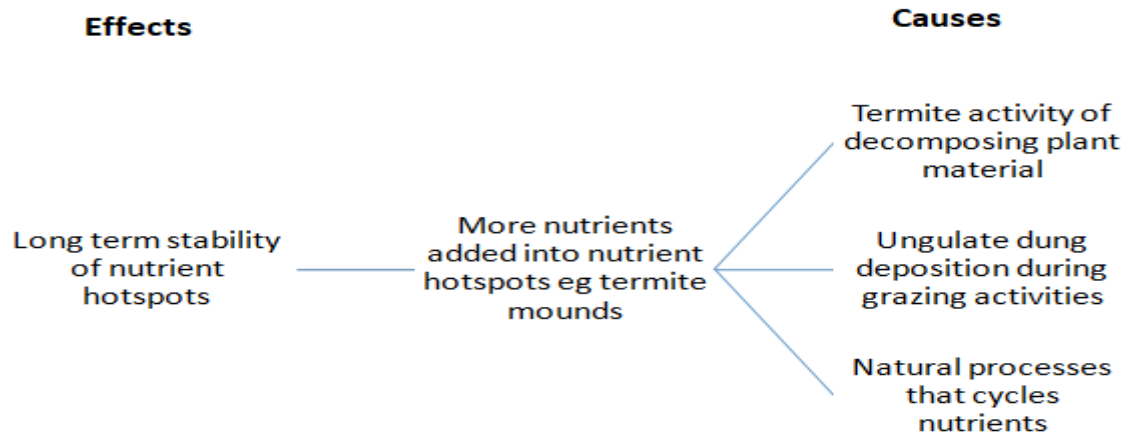

Figure 1: The cause-effect relationship diagram of nutrient depositions around hotspot areas

1.2 Statement of the problem

Termite mounds play an important role in many savanna ecosystems as they can enrich soils that are generally characterized by a low reserve of weatherable minerals (Davies *et al*., 2016; Jones *et al*., 1994; Jouquet *et al*., 2016). The termite activity of decomposing dead plant materials directly or indirectly modifies the availability of nutrients for other organisms including ungulates (Jones, 1994). Probably, due to this nutrient enrichment through termites, the surrounding vegetation might be preferred by ungulates and other organisms. However, little is known about how strongly these mounds contribute to vegetation quality, to associated ungulate foraging activity and, consecutively, to the overall heterogeneity of the landscape (Davies *et al*., 2016). Only few studies have been done on the variation of various essential nutrients such as N and P in termite mound soils compared with controls (López-Hernández, 2001), with no literature in Miombo ecosystem. Hence, there is a need for understanding the ecological importance of termite mounds and grazing lawns (Jouquet *et al*., 2016), especially in miombo ecosystem.

Literature shows that termite mounds in savanna are sites of high soil nutrient concentrations compared to nearby soils (Carneiro *et al*., 2018; Holt & Lepage, 2000 and Sileshi *et al*., 2010). However, mound structure and termite behaviour together prevent the re-distribution of enriched soil from termite mounds to the surrounding landscape (Holt & Lepage, 2000). To date, no study has identified whether termite mounds are important for ungulates in this miombo ecosystem. Further, no study has identified, which ungulate species in this ecosystem are strongly attracted to these termite-shaped features.

Grazing lawns are areas located on nutritious soils that have been intensively used by ungulates, leading to fresh regrowth and nutritious grasses (McNaughton, 1985). These areas are highly important in ecosystems as they support large numbers of ungulates (Seagle *et al*., 1992). Grazing lawns patches have also been observed in Issa valley but no study has identified which animal species use these sites and what makes the lawns so attractive for ungulates in this miombo ecosystem.

Grazing ecosystems are among the earth's most endangered savanna habitats (Frank *et al*., 1998), highly impacted by anthropogenic activities. In the Issa valley ecosystem, wildlife conservation is challenged by the local communities looking for various ways to improve their livelihoods (Wilfred & Maccoll, 2010). Elsewhere, grazing areas have often been

converted into food producing areas to support a rising human population and their domestic ungulates (Frank *et al*., 1998).

Various factors like climate, soil type, grass species and grazing can affect dynamics of nutrients (Silveira *et al*., 2012). Up to now, few studies have combined ungulates and nutrient re-distribution (Moe & Wegge, 2007) that might improve grazing management and nutrient availability in grazing areas (Haynes & Williams, 1990). Re-distribution extent to nearby soils usually depends on nature of the mounds, soil erosion as well as nutrient leaching rates (Holt & Lepage, 2000). Re-distribution rates can also be triggered by ungulates as agents from one area as they excrete in resting or sleeping sites (Frank & Evans, 1997; Jewell *et al*., 2007; Singer & Schoenecker, 2003 & Veldhuis *et al*., 2016). However, there is little evidence on whether the approximate foraging location from where they were deposited.

1.3 Rationale of the study

Only few studies have been done on the dynamics of various elements such as C, N and P in termite mound soils compared with controls (López-Hernández, 2001), with no literature in Miombo ecosystem. Hence, there is a need for understanding the ecological importance of termite mounds (Jouquet *et al*., 2016) especially in miombo ecosystem. To date in Western Tanzania no study has identified whether termite mounds are important for ungulates in this miombo ecosystem. Furthermore, no study has identified, which ungulate species in this ecosystem are strongly attracted to these termite-shaped features. This study will fill the existing gap in miombo ecosystem.

Furthermore, grazing lawns patches have also been observed in Issa valley but no study has identified which animal species use these sites and what makes the lawns so attractive for ungulates in this miombo ecosystem. This study will show different ungulate species utilizing grazing lawns in different seasons and how they can be created in habitat fragmented and degraded areas for supporting wild and domestic ungulates. Furthermore, it will show factors in their own or in combination that attract various ungulates in these hotspots.

Furthermore, this study will expound how nutrients from these hotspots are accumulated or they are rather re-distributed away from nutrient hotspots. There is a need of understanding nutrient re-distribution from these important feeding grounds in Western Tanzania. Understanding of this information is important for the long-term monitoring and maintenance

of nutrient rich and productive hotspot areas. This study will clearly show the importance of conserving various nutrient hotspots within a grazing ecosystem, which might be essential foraging resources for ungulates in the miombo ecosystem of Western Tanzania.

1.4 Objectives

1.4.1 General objective

To understand the importance of nutrient hotspots for wild grazing ungulates in a Miombo Ecosystem of the Issa valley, Western Tanzania.

1.4.2 Specific objectives

(i) To compare plant species richness and diversity on nutrient hotspots (termite mounds and grazing lawns) as well as further away from these hotspots (controls).

(ii) To compare chemical properties of soil and grasses on nutrient hotspots (termite mounds and grazing lawns) as well as further away from these hotspots (controls).

(iii) To assess ungulate grazing frequency on nutrient hotspots (termite mounds and grazing lawns) as well as further away from these hotspots (controls).

(iv) To experimentally identify factors that could lead to the attractiveness of these various nutrient hotspots for grazers.

(v) To understand the wide-reaching nutrient redistribution through grazers foraging on the nutrient hotspots based on stable isotope analysis.

1.5 Research questions

(i) Do areas around termite mounds and on grazing lawns have higher plant productivity, nutrient contents, richness and diversity compared to areas away from nutrient hotspots (controls)?

(ii) Is grazing frequency by ungulates around termite mounds and on grazing lawns higher than in areas away from these nutrient hotspots (controls)?

(iii) Are chemical properties of soil and grass around termite mounds and grazing lawns higher compared to areas away from these nutrient hotspots (controls)?

(iv) What are the factors that attract ungulates towards nutrient hotspots?

(v) Are the nutrients deposited closer or further away from these nutrient hotspots via dung of ungulates?

1.6 Significance of the study

The study aims to understand the importance of nutrient hotspots on a small scale (foraging patch scale) as well as their contribution to heterogeneity on a habitat and landscape scale in miombo ecosystem. In this study, ungulate species that are most strongly dependent on different types of nutrient hotspots in the miombo ecosystem of Issa valley will be identified. Furthermore, the study will show how various factors on their own or in combination contribute to the existence and attractiveness of various hotspots in the study area, hence, understand the possibility of creating and maintaining nutrient hotspots in nutrient poor and habitat fragmented areas. Furthermore, the study show the role done by termite mounds in contributing to habitat heterogeneity, which not only supports ungulates but also other animals like chimpanzees (*Pan troglodytes schweinfurthii*) in the Issa valley, a charismatic species that is of high conservation concern. Thus, the study is highly relevant in identifying the importance of hotspots for focus animals in a highly diverse area of a miombo ecosystem that needs protection (Gonçalves *et al*., 2017; Gumbo *et al*., 2018; Jew *et al*., 2016). Overall, using novel technologies, this study highlights the importance of conserving various nutrient hotspots within an otherwise rather nutrient-poor grazing miombo ecosystem. These hotspots might be essential foraging resources for ungulates in Tanzania and across African savannas in general. Hence, this knowledge will improve grazing management and nutrient availability in grazing areas (Haynes & Williams, 1990).

1.7 Delineation of the study

This study focused on assessing importance of nutrient hotspots (termite mounds and grazing lawns) for wild grazing ungulates in miombo ecosystem of the Issa valley, Western Tanzania. Thus, the study did not consider different termite species.

CHAPTER TWO

LITERATURE REVIEW

2.1 Importance of nutrient hotspots

Nutrient hotspots (Grant & Scholes, 2006; Shantz *et al*., 2015) are crucial elements in the feeding ecology of wild ungulate species in heterogeneous savanna systems (Treydte *et al*., 2006). Nutrient thresholds for metabolism maintenance in ungulates are often only reached through specific forage preferences (Arsenault & Smith, 2008; Shahar, 1991). Termites *(Macrotermes* spp*)* act as soil ecosystem engineers by enhancing decomposition and mineralization processes, hence promoting soil turnover and influencing soil nutrient distribution (Grohmann, 2010). Termite mounds in a South African savanna system have been shown to be nutrient hotspots that support a high plant diversity and are expected to offer higher nutritional value to wildlife than the surrounding environment (Davies *et al*., 2014). In Kruger National Park, South Africa, ungulates were found not to forage uniformly across the landscape but rather to select areas that have high nutrients and very low predation risks (Davies *et al*., 2016). Around termite mounds, rainfall sweeps remarkable amounts of nutrient-rich soil to immediate surroundings (Lepage, 1984), which are then often colonized by grass species with a high nutrient demand (Dangerfield *et al*., 1998). High forage quality and high plant diversity due to increased soil nutrients around termite mounds, therefore, is expected to lead to higher grazing pressure by ungulate (Dangerfield *et al*., 1998; Lamprey, 1963).

A locally high grazing pressure has also been associated with grazing lawns, which are characterized by the presence of short grass species, as well as maintained and influenced by high feeding activities (Archibald, 2008; Cromsigt & Olff, 2008; Hempson *et al*., 2015; McNaughton, 1984). Within grazing lawns, grazers keep grasses short and the freshly regrown grasses with low stem proportions are highly palatable (Coetsee *et al*., 2011; Hempson *et al*., 2015; McNaughton, 1984). These lawns are normally self-maintaining as grass quality increases through the cycle of grazing-dung deposition (Lamprey, 1963; McNaughton, 1984). Various grazers such as the wildebeest (*Connochaetes taurinus*) are attracted by short green grasses of high nutrient content (Bremm *et al*., 2016; Eby *et al*., 2014; Mandlate *et al*., 2019).

2.2 Nutrient concentration, availability and re-distribution in hotspots

The grazing ecosystem is among the earth's most endangered terrestrial habitats (Frank *et al*., 1998) often encompassing savannas that are characterized by a continuous layer of palatable and unpalatable grass species (Grant & Scholes, 2006). Nutrient availability in grasses has long been studied and found to be important for various ungulates (Frank *et al*., 1998; McNaughton, 1985; Treydte *et al*., 2011). A substantial amount of the nitrogen (N) and phosphorus (P) that are found in grasses are recovered in the dung and urine (Haynes & Williams, 1990). Therefore, nutrients are carried back to grasses through dung defecation and represent important sources of N and P for grasses (Haynes & Williams, 1990). Dung mineralization is higher than that of plant litter, hence, the former strongly fosters nutrient cycling (Thomas, 1992). Nutrient concentration is often high in areas of high grazer visitation (Sollenberger, 2009). These areas of high grazer visitation are, for example, grazing lawns (Cromsigt & Olff, 2008; McNaughton, 1985). These nutrient hotspots have been shown to attract grazers. Another such nutrient hotspot is represented by termite mounds Davies *et al*., (2016) and Reid (2012). Since termite mounds are high in nutrients, one would expect that grazers favorably forage there and might, thus, also deposit more urine and dung on or next to these hotspots. Dung and urine depositions affect chemical composition of soil and grasses (Moe & Wegge, 2007) as well as plant productivity (Haynes & Williams, 1990) these nutrient hotspot areas strongly support ungulate species especially in nutrient poor savanna soils. Generally, in Eastern and Southern Africa, open grasslands containing termite mounds, grazing lawns (Ben-Shahar, 1991; Burkepile *et al*., 2013; McNaughton, 1984a; Mobæk *et al*., 2005) and containing few tall trees (Treydte *et al*., 2008) were found to be areas preferred by the ungulates to forage on. As foraging by ungulates has also strong seasonal patterns (Sheehy & Vavra, 1996), the nutrient hotspots might be of seasonal importance and their use by ungulates might shift across the year. However, the spatial and temporal nutrient cycling around these hotspot areas, from soils via plants to ungulates and back into soils, is difficult to trace and quantify (Jobbágy & Jackson, 2001).

While the importance of grazing lawns for ungulates in savanna has been studied (McNaughton, 1983; McNaughton, 1984; Veldhuis *et al*., 2014), only few experiments done in the field exist that quantified the extent to which these lawns attract grazers in nutrient poor areas (Davies *et al*., 2016). In addition, the extent to which the grass layer around these hotspots is consumed by grazers is poorly understood. Particularly in the Miombo ecosystem

of the Issa valley, where termite mounds are important for chimpanzee *(Pan troglodytes schweinfurthii)* foraging activities (Almeida-Warren *et al*., 2017; Stewart & Piel, 2014), little is known about the importance of the former for sympatric ungulates. Moreover, termite mound and grazing lawn soils have never been compared experimentally for their potential in enhancing grass growth and quality.

2.3 Camera trap usage for understanding ecological processes

Direct observation of various ungulates in their natural environment is very difficult as some of the animal species are nocturnal and very shy (Frädrich, 1974; Rahman *et al*., 2016). Camera traps provide a wide range of unexpected results, which can be incorporated in long-term monitoring programs (Stein *et al*., 2008). They have been used in various ecological studies (Kelly & Holub, 2008; Kolowski & Forrester, 2017; Rovero *et al*., 2014), providing great understanding of ecological processes (Sollmann, 2018), also being a non-invasive method for ecological data collection (Stein *et al*., 2008). They have been used to understand different variables of interest in an ecosystem such as species abundance, diversity and distribution of various mammals (Wearn & Kapfer, 2017). Furthermore different behavioral activities of various mammals can be understood using camera traps (Burton *et al*., 2015). The number of camera traps deployed in a particular study determine the amount of data that can be collected (Wearn & Glover-Kapfer, 2017) which are often reliable and with unbiased activity (Tobler *et al*., 2009) during day and night, dry and rain season. Such widespread applications of camera traps are generating novel data applications, and promote the potential for methodological standardization which has made it a cornerstone of global biodiversity monitoring initiatives (Burton *et al*., 2015).

Camera traps have been used in the Udzungwa Mountains, Tanzania, to study large to medium mammalian species richness and composition, which has been threatened by hunting and habitat loss (Rovero *et al*., 2014). Also, this technique has been used in an insular ecosystem of Melbourne, Australia, to identify rodent species causing significant damage to the island environment (Rendall *et al*., 2014). Five Amazonian ungulate species were studied using camera traps to understand their activity patterns and mineral licking behaviour (Tobler *et al*., 2009). However, camera placement decisions in different study plots are a critical consideration and are a potentially large source of bias in detection rates (Kolowski & Forrester, 2017).

In animal behaviour, camera traps have been used to understand anti-predator responses by ungulates in different habitat or near threat of predator (Kuijper *et al*., 2014). In Ireland, camera traps were used to understand activity pattern of different mammal species and their association in predator-prey relationship (Caravaggi *et al*., 2018). Human-elephant conflict aspects in Udzungwa Tanzania were detected via camera traps to understand behaviour of individual elephant populations that were more likely to forage on crops and to understand their temporal patterns of visiting farms (Smit *et al*., 2019). Generally, camera trap data analysis can provide a solid ecological assessment of mammalian communities that can be systematically replicated across sites (Rovero *et al*., 2014). However, to maximize the detection rates of a particular species or guilds (e.g. carnivores), camera traps should not be placed on roads and trails as they will not provide reliable estimates of relative abundance of sympatric species (Mann *et al*., 2015). Hence, Camera trap usage allows practitioners to concurrently survey across a wide range of species and their respective habitats, providing data that may be of great utility in informing subsequent investigations and/or answering important ecological questions (Caravaggi *et al*., 2018).

2.4 Indirect observation in understanding ecological processes

Indirect observations including dung depositions, track signs and grass tufts usage have been widely used for different ecological studies (Treydte, *et al*., 2006; Veldhuis *et al*., 2017). In a study that was done in Kwa-Zulu Natal, South Africa, dung deposition from large herbivores was used to understand a nutrient re-distribution process, where large dung depositions were found in different places where the animals graze, hence, increasing plant nutrient availability in terrestrial ecosystem (Veldhuis *et al*., 2017). Another study that was done in Kenya and South Africa was assessing habitat use of wild and domestic ungulates beneath-canopy vegetation where dung depositions and tufts usage were used during assessment (Treydte *et al*., 2010). Indirect observations were also used to assess habitat use of the common warthog (*Phacochoerus africanus*) in Tanzania (Treydte *et al*., 2006). Furthermore, the role of pastoralists on savanna ecosystem in Amboseli Kenya was assessed based on ungulate dung that was deposited in abandoned pastoral settlements (Muchiru *et al*., 2008).

Hence, various studies elsewhere have used indirect methods for data collection (Archibald *et al*., 2005; Gillet *et al*., 2010; Muchiru *et al*., 2008) but few enriched their indirect methods with camera trap footage (Rahman *et al*., 2016). Enriching data collection in this study using

camera traps fills the gap by identifying the responsible ungulate species (Sollmann, 2018) whose dung's and tracks form part of the data in the findings.

2.3 Using stable isotopes in re-tracing nutrients

Stable isotope analysis has recently been used for various ecological studies in food chains, trophic relationships, re-source allocation and various food webs (Boecklen *et al*., 2011; Finlay & Kendall, 2008; Frank & Evans, 1997 & Werner *et al*., 2012). Isotopic signatures of C and N are used as tracers in ecosystems (Lepoint *et al*., 2004). These signatures, which are represented by potential plant food sources, and the fact that the isotopic composition of an animal tissue is strongly determined by the isotopic composition of its food, allow the use of isotopic ratios as food web integrators in various ecosystems (Boecklen *et al*., 2011; Lepoint *et al*., 2004). As analysis method, the addition of labeled substances can be used as tracer at levels outside the natural ranges (Lepoint *et al*., 2004). Currently, various sub disciplines have been developed out of using isotopes, including isotope mixing models, isotopic routing models, and compound-specific isotopic analysis (Boecklen *et al*., 2011) all of which aim at understanding various complex and dynamic ecological processes in different ecosystems (Bouillon *et al*., 2011).

Regardless of currently advancing isotope usage in ecology, most attention has been given to aquatic systems (Finlay & Kendall, 2008) while little has been done in using stable isotopes for terrestrial systems, particularly in Eastern Africa (Treydte *et al*., 2006). Stable isotopes were also used in Kruger National Park, South Africa, to understand feeding patterns of elephants (*Loxodonta africana*), particularly when they were switching between grass and browse, where results reflected a shift in diet from higher C_4 grass intake during the wet season months to more C_3 browse-dominated diets in the dry season (Codron *et al*., 2011).

Furthermore, another isotope study was done in Kenya, where a hair sample from rhino was used to determine their diet composition, water deficit and illegal wildlife materials (Cerling *et al*., 2018) with results showing differences in diet across geographical areas. Similarly, another study was done in Laikipia, Kenya to identify diet differences between endangered Grevy's zebra (*Equus grevyi*) sharing habitat with Plain zebra (*Equus quagga*) (Kleine & Fox-dobbs, 2010) where results indicated diet partition between them. All these studies aimed at understanding ecological management options for various mammalian species. Similarly, Termites in Kenya were also found to influence atmospheric nitrogen fixation, using stable

isotopes based on ^{15}N abundance in African savannas (Fox-Dobbs *et al*., 2010) indicating their importance as drivers of community and ecosystem structure. Hence, recent advances in experimental tracer studies using isotopes offer a lot of possibility to study different fundamental ecological processes involved in C and N cycles, particularly at the community scale level (Lepoint *et al*., 2004).

Previous to this isotope technique usage, ungulates have been studied for decades, yet debate still exists about their diet composition across Africa (Sponheimer *et al*., 2003). Among the challenges in many studies was to clearly set the connection between the ungulate species of interest foraging on a diet that differs in isotopic composition and choosing tissue that will yield the appropriate record of the past feeding location (Hobson, 1999). As natural tracers, stable isotopes can be used in showing plant-animal relationships and truly reflect food sources, habitat, distribution and movement in terrestrial ecosystems (Jianzhu *et al*., 2004). This technique also provides an ideal tool to understand food web relationships, nutrient cycling and ungulate community structure because of isotopic fractionation during the processes of nutrient assimilation by animals (Bouillon *et al*., 2011; Jardine *et al*., 2017). Further, current topic of interest of ungulates is on effect of nutrient cycling both in natural and agricultural ecosystems (Tonn *et al*., 2019).

CHAPTER THREE

MATERIALS AND METHODS

3.1 Study area

The Issa valley is found in western Tanzania, in Tanganyika district, Katavi Region. The valley is about 90 km^2 consisting of wide valleys and steep mountains from 900-1800 masl (Piel *et al*., 2015). The dominant vegetation in the area is Miombo woodland (*Brachystegia, Isoberlinia* and *Julbernardia* species), with interspersed swamps, grasslands, thickets and closed canopy forests, (Piel *et al*., 2015; Stewart & Piel, 2014). There are two seasons: wet (November-April) and dry (May-October), with >100 mm and <100 mm of rainfall, respectively (Stewart & Piel, 2014; FitzGerald, 1960). Some large mammals found in the study area are Lichtenstein's hartebeest (*Alcelaphus lichtensteinii*), Roan antelope (*Hippotragus equinus*), Common waterbuck (*Kobus ellipsiprymnus*), Klipspringer (*Oreotragus oreotragus*), Warthog (*Phacochoerus africanus*), Blue duiker (*Philantomba larvatus*), Bushpig (*Potamochoerus larvatus*), Reedbuck (*Redunca redunca*), Common duiker (*Sylvicapra grimmia*), African buffalo (*Syncerus caffer*), Derby's eland (*Tragaphus derbianus*) and Bushbuck (*Tragelaphus scriptus*) (Piel *et al*., 2018).The area does not have formal protective status (Piel *et al*., 2018) and is surrounded by villages (Uvinza, 70 km) as well as recent villages that emerged from a former refugee settlement (Mishamo) which was established in the 1970s (Piel *et al*., 2015). In the surrounding ecosystem human activities such as small scale logging, agriculture, snares and camping activities have been documented (Piel *et al*., 2018; Stewart & Piel, 2014). This study complied with Tanzanian Wildlife Research Institute (TAWIRI) ethical regulations and permission was granted from both TAWIRI and the Tanzanian Commission for Science and Technology (COSTECH).

3.2 Data collection

3.2.1 Grass characteristics on hotspots and controls

Ten active termite mounds, covered with grass, that were not close to water bodies (i.e., more than 100 m away from water source) or from big trees that were on average (±SE) more than 9.0 ± 0.3 m tall and had a canopy radius of 5.5 ± 0.2 m (Treydte *et al*., 2010) to avoid potential confounding factors were selected. Their ten respective control sites were randomly selected and placed 100 m away from the mounds (Mobæk *et al*, 2009) and away from big

trees. Circumference and approximate height were recorded for each termite mound. Transects were laid down from each termite mound centre in all four compass directions (N, S, E,W), and along each transect, one 1 x 1 m^2 quadrat each was placed at 2 m, 12 m and 22 m distance away from the base of the mound (Davies *et al*., 2014). In each quadrat, grass communities, i.e., species and their respective basal cover, on and around the mound were surveyed (Arshad, 1982; Davies, Robertson *et al*., 2014). Furthermore, in each quadrat, an additional 0.5 x 0.5 m^2 quadrat was used, where in each quadrat; study measured standing biomass by harvesting above ground grass biomass and recording their dry weight between May 2016 and October 2017. Grass biomass was measured in February, May and September. In each quadrat, there were 4 different cardinal points of 50 x 50 cm^2 quadrats. At each sampling event, a new location of the four subplots was used. At a distance of 100 m away from each termite mound, transects and quadrats of the same size were established as a control. The same procedure was done for grazing lawns at distances of 20 m, 40 m and 60 m from the grazing lawn centre and their respective control sites were at a distance of 100 m from the grazing lawn edge. Grass identification in all study plots was done in the field with the assistance of a botanist and literature (Oudtshoorn, 2002). The study measured vertical grass height at four different points within each sampling quadrat, thereafter, averaged the height measurement for all sampling plots (Eby *et al*., 2014). Additionally, grass greenness was assessed based on score scales ranging from scorched grass (1), pale green (2), green (3) and deep green (4) (Gosling *et al*., 2016; Mandlate *et al*., 2019; Treydte *et al*., 2013). However, ten termite mound areas and control sites in Miombo vegetation as well as some areas in grazing lawns were heavily affected by fire from July 2017 onwards and grass assessment was not possible thereafter (plate 3).

3.2.2 Grass and soil chemical properties

Grass and soil samples from ten termite mounds, ten controls, six grazing lawns and six controls were collected for measurement of available nitrogen (N) and phosphorus (P) contents, i.e., essential nutrients for ungulates (Grant & Scholes, 2006; Treydte *et al*., 2013). In termite mounds, grass and soil samples were collected at a distance of 2 m, 12 m and 30 m, while in grazing lawns were collected at 20 m, 40 m and 60 m away from the hotspot centre. Soil samples were collected wet-season from 0 to 10 cm depths by combining three cores/plot depth using a stainless steel hand trowel (Koenig *et al*., 2000). Grass samples were clipped using scissors directly above the ground at different plots, inflorescence if present removed

(Kilcher, 1981) placed in paper bags thereafter air dried under the shade (Hayhoe and Jackson, 1974a; Phang *et al*., 2015; Ludwig *et al*., 2001; Zaki *et al*., 2017) stored in paper bags and transported to the Core Facility Centre at the Hohenheim University, Germany for analysis. Soil samples were ground using mortar and pestle, while grass samples were ground using Fritsch's mill with a sieving ring of 0.5 mm. Samples of 0.25 mg of soil and grass were weighed, digested under microwave ultra clave, (dos Santos *et al*., 2012) thereafter introduced into ICP-OES (Vista Pro) (Daly & Fenelon, 2017; Makita, 2014; VaiVäisänen *et al*., 2008) to determine total N and P contents in soil and grass respectively. A total sample of 101 grasses and 24 soil composite mixtures from 122 different plots, were analysed.

3.2.3 Ungulate grazing frequency through indirect observation

In already established plots around termite mounds, grazing lawns and their respective controls, grass tuft use was assessed and estimated as percentage in all quadrats (Grant & Scholes, 2006; Treydte *et al*., 2011) in February, May and September 2017 to cover various grass growth periods throughout the year. Utilized/eaten tufts were identified as grass that had been eaten partially or fully by the animal (Treydte *et al*., 2010). Grass preference indices were assessed within each quadrat as 0 (no grass available), 1 (no grazing i.e., none of the grass tufts show bite marks), 2 (moderate grazing/very light grazing i.e., partially eaten), 3 (heavy grazing) and 4 (intensely grazing) (Archibald, 2008). However, ten termite mound areas and control sites in miombo vegetation as well as some areas in grazing lawns edges were heavily affected by fire from July 2017 onwards and, hence, termite mound data from July 2017 were dropped from analyses. Presence of different ungulate species was determined by recording cumulative dung depositions (graded as 1-fresh, 2-recent, 3-old) and tracks i.e., footprints (Curtis, 1995; Liebenberg, 1990), (plate 4). Tracks for an animal that was moving in one direction were considered as one event (plate 5). After recording evidence, signs were removed to avoid re-counting. Dung (plate 4) and tracks (plate 5) were identified using Stuart and Stuart (2006) with the assistance of experienced Tanzanian field assistants.

3.2.4 Ungulate grazing frequency using camera traps

Moreover, to enhance grazing intensity data in this study two types of motion detecting, infrared triggered cameras (Reconyx HC600 Hyperfire and Bushnell) (Rendall *et al*., 2014; Schieltz, 2017) twelve in total were randomly placed in pairs, with one camera on the hotspot

and one in the control areas (Kolowski & Forrester, 2017). Hotspots and controls used were the ones already selected previously and their locations were mapped using GIS (Tobler *et al*., 2008; Zlatanova & Popova, 2018). Both camera locations had similar ground cover characteristics (Kolowski & Forrester, 2017), all cameras were mounted 40 cm above the ground (Kolowski & Forrester, 2017 & Rendall *et al*., 2014) and about 5 m away from but facing the nutrient hotspot centre (Mann *et al*., 2015). About 1 m^2 of vegetation was cleared at each camera to avoid triggers caused by moving vegetation (Kelly & Holub, 2008 & Rendall *et al*., 2014). Distance between cameras was at least 100 m (Kolowski & Forrester, 2017). Generally, two cameras each were placed on termite mound areas and control sites, three each on grazing lawn areas and control sites, thereafter rotated every month to cover all 10 termite mounds, 10 controls, 6 grazing lawns and their 6 controls Fig. 1. Cameras took one photograph per second after the object/animal passed in front of the camera and emitted the required level of infrared radiation to capture within the field of view (Wearn & Glover-Kapfer, 2017). Physical attributes between hotspots vs control sites were the same, use of camera traps to compare ungulate usage of these sites considered to be appropriate method (Stein *et al*., 2008).

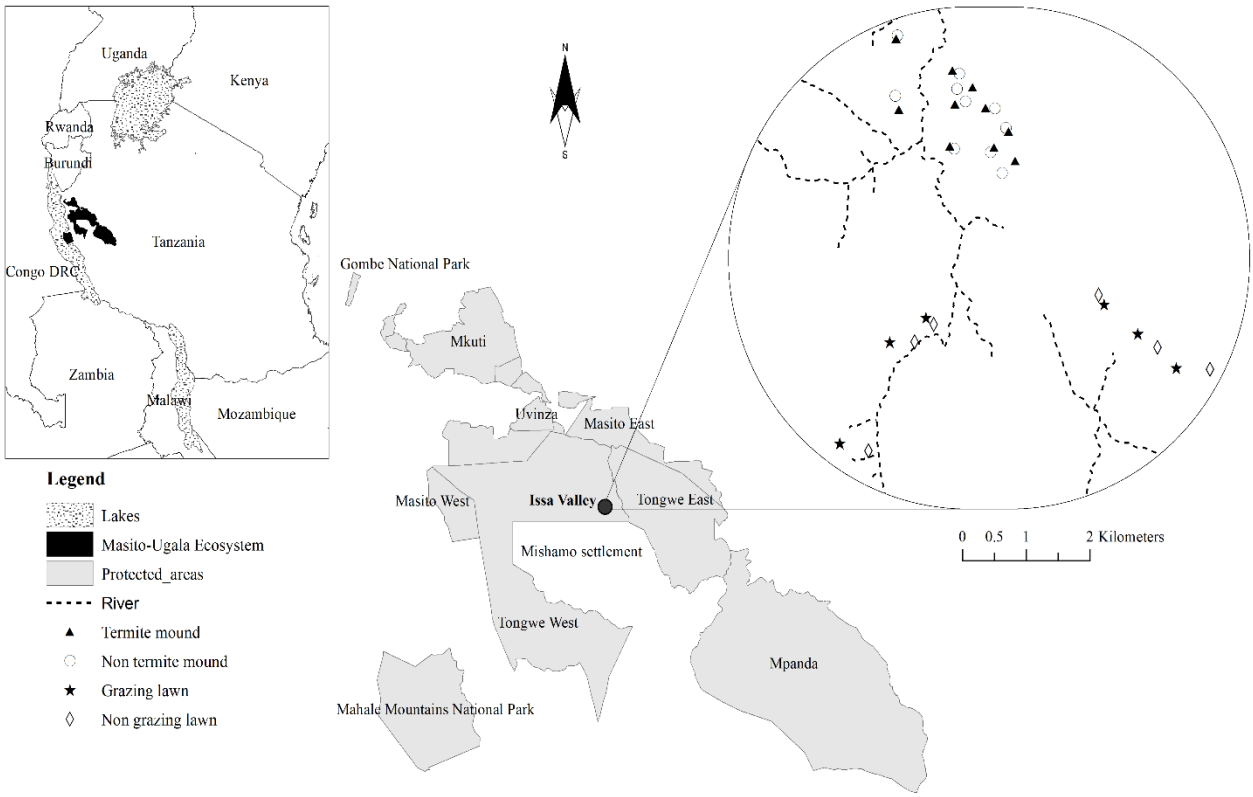

Figure 2: Map of Issa valley, Western Tanzania, showing camera trap deployed points

3.2.5 Hotspot attractiveness experiments

In addition, experimental plots in the field were created to tease apart the factors that might contribute to the attractiveness of nutrient hotspots. Ten quadrats each of 5 x 5 m^2 were fertilized with NPK fertilizer (ETG Input NPK 17-17-17 400 g/m^2), cut to ground level, and irrigated with 10 l/m^2 once, summing up to 40 experimental plots in total. Experimental plots selected were neither too close to shade nor to water bodies to avoid potentially attractive confounding factors. In addition, the most dominant grass species (*Hyparrhenia hirta*) was sampled before setting up the experiment and after the experiment to assess the nutrient status (N, P content). In addition, the study assessed the extent of grazing (in %) in each plot visually. Among the dominant grass species found around termite mounds, the study set a grass preference scale score from 0 (no grass) to 5 (intense grazing). Across all sample plots in hotspot attractiveness sites, visitations of various ungulates (grazers) were observed for a period of one year (September, 2016 - October 2017) in and around experimental plots and their respective control sites in the Issa valley through indirect observations i.e., by recording dung depositions and tracks (Treydte *et al*., 2010). The presence of different wildlife species was determined by recording cumulative dung depositions as well as tracks and recording the age of the signs. Similarly, tracks for an animal that was moving in one direction were considered as one event. After recording evidence, similar to previous study sites dung or track signs were removed to avoid re-counting. Identification of the dung and tracks was done according to Stuart and Stuart (2006) with the assistance from experienced Tanzanian field assistants.

A pot experiment was conducted in Issa valley, Western Tanzania during January, 2017 - May 2017 for a total of 61 days. Thirty pots (30 cm diameter) (Shaheen *et al*., 2010) made with compostable plastic bags (Vaverková *et al*., 2014) were used to decaplicate (n=10) as replicates (Nishimura *et al*., 2006) three treatments. Each pot was filled with 5 kg homogenized compost mixture soil taken from 0-300 mm soil layers (Mulidzi *et al*., 2016), after grinding and screening though a 0.6 mm sieve (Utkhede & Rahe, 1979). The soil was taken from 5 termite mounds, 5 grazing lawns and 5 controls. Ten seeds of *Cynodon dactylon* collected from Nelson Mandela African Institution of Science and Technology were sown at equal distance in each pot at 2 cm depth (Shaheen *et al*., 2010) by hand on January 15, 2017. Pots were exposed to the natural environment (Hendrik *et al*., 2012) and water was added ad libitum. After seedling emergence, extra seedlings were removed (Shaheen *et al*., 2010) to

maintain ten plants as replicates per pot. Grass height was measured using a ruler after every 3 days. *Cynodon dactylon* grass was harvested on 30 May, 2017, by cutting the plants directly above the soil surface (Shaheen *et al*., 2010). Fresh and dry grass biomass were measured for each pot separately, thereafter each treatment was kept in separate paper bags and transported to the Core Facility Centre at the Hohenheim University, Germany for analysis. Grass samples were ground using Fritsch's mill with sieving ring of 0.5 mm. A 0.25 mg of soil and grass was weighed in each sample, digested under microwave ultra clave (dos Santos *et al*., 2012) thereafter introduced into ICP-OES (Vista Pro) (Daly & Fenelon, 2017; Makita, 2014; VaiVäisänen *et al*., 2008) to determine total N and P contents.

3.2.6 Nutrient re-distribution via isotope analyses

A quadrat of 50 m^2 was created centering on the already selected termite mound. Transects were laid from each termite mound centre in all four compass directions (N, S, E, W). To test whether dung signature deposited around termite mounds is more closely related to termite mound grass signature than to non-termite mound grass signature, ^{15}N-Urea was foliarly sprayed (Carlo *et al*., 2009) on grasses around five termite mounds within a quadrat of 2 m^2, with the mound acting as a central point. The urea was re-traced back in the dung collected around hotspots within a radius of 30 m^2 by being reflected by corresponding δ15N values. In all sprayed termite mounds every 2 days after spraying urea, fresh dung pellets (4-6) from Hartebeest within a 30 m radius were collected for three weeks consecutively. After collecting dung sample, remainders were distributed within the soil to avoid re-sampling. Grass samples were also collected from sprayed grasses near the termite mounds and at a distance of 100 m away from urea sprayed termite mound acting as a control. A total of 32 dung pellets and 32 grass samples were collected, air dried (Carlo *et al*., 2009 & Miranda *et al*., 2014), stored in paper bags and analysed at the Food Chemistry Institute, University of Hohenheim, Germany. Grass and dung samples were oven dried at 70^0C for 48 h (Carneiro *et al*., 2018), homogenized with a milling machine (Namiesnik *et al*., 2003) and 0.2-0.3 mg were placed in a tin capsule (Reitsema, 2015) ready for isotopic analysis. The delta N was determined by an Elemental analyzer Intergrated via Thermo Finnigan continuous flow with Isotope Mass spectrometer (Ogawa *et al*., 2010; Reitsema, 2015). N isotope ratios were calculated as δ^{15}N where δ represents the proportional deviation in parts per thousand (‰) from the reference standard Glutamic acid and USGS40 (Qi *et al*., 2016): δ= 1000((Rsample/Rstandard) - 1), where R was the ratio of heavy to light isotopes (Markow *et*

al., 2000). Each sample was replicated once to avoid errors (Peters, 2001; Reitsema, 2015). Standard deviations for ^{15}N were less than 0.1‰ (Rennie *et al*., 1976).

3.3 Data analysis

Grass species richness and diversity indices data was averaged for termite mounds, grazing lawns and their respective controls, thereafter compared using t-test in Paleontological Statistics (PAST) software (Hammer *et al*., 2001). Grass height and biomass from areas on termite mounds and grazing lawns were tested for normality and compared against 2 m, 12 m and 100 m, and for grazing lawns at 20 m, 60 m and 100 m respectively using one-way ANOVA. Grass greenness and basal cover on termite mounds and grazing lawns was compared with that of controls using t tests and one-way ANOVA. Furthermore, a generalized linear mixed model (GLMM) was also applied to evaluate the effect of site (random factor), location (hotspot vs control) and season (wet vs dry) and their interaction with grass biomass. Grass preference index scores of different species were averaged for each grass species separately, divided by the highest grazing score (5) thereafter, computed into percentage. A generalized linear mixed model was further used to evaluate the effect of nutrient hotspots site i.e. hotspot vs control and their distance i.e. closeness to the nutrient hotspot and their interaction with nutrient content (N). The study tested the interaction between location, distance, season and nutrient availability against tufts usage estimates using GLMM. *Cynodon dactylon* grass height and nutrient contents after harvesting was tested for normality then compared across pots with termite mound, grazing lawn and control soils using one-way ANOVA. In the fertilizing experiment, grass N and P content levels were measured before setting the experiment and after application of fertilizer, tested for normality then compared across treatments using a one-way ANOVA. The study also compared ungulate presence (tracks and dung) across fertilized, clipped (Jamet, 2016) and control plots using one-way ANOVA after normality test. Grass height and tuft usage estimates were compared across fertilized, clipped and control plots, as well as termite mounds, grazing lawns and their respective controls using a one-way ANOVA. Ungulate presence (tracks and dung) was compared between hotspots and controls as well as over dry and wet season using one-way ANOVAs. Tukey's Post-hoc tests were used in all statistical tests, with significant levels set at $\alpha = 0.05$. The software used was Origin Pro 8 (Serrano *et al*., 2011) and SPSS version 20 (Li *et al*., 2017).

The presence of the three grazer species based on cumulative dung depositions was averaged over the ten termite mounds, six grazing lawns and their respective control sites. This was then tested for normality and compared between hotspot and control sites as well as between season using one-way ANOVA. The same was done for the average number of camera trap events. Camera trap data were grouped into months, and categorized into dry and wet season for both hotspot and non-hotspot areas. Furthermore, isotopic signatures of urea sprayed grass and isotopic signatures of dung deposited within 30 m from the sprayed grass were compared using one-way ANOVA (Miranda *et al*., 2014). Tukey's Post-hoc test was used in all statistical tests, significance levels were set at $\alpha = 0.05$. Software used was Origin Pro 8 (Serrano *et al*., 2011).

In camera traps footage, animal presence intensity level were calculated as the total number of animal images captured counted as number of events per hour in a particular plot over the year period (Zavaleta *et al*., 2014) which means if the same animal was photographed more than once by the same camera within 1 hour, this was considered as one event (Tobler *et al*., 2009) the study thereafter compared total number of animal events captured in hotspot areas versus total number of animal events captured in non-hotspot areas over the year period. Each of the cameras stamped date and time in each of the photograph, this was important in separating events and in preventing double counting (Kelly & Holub, 2008). The average number of camera trap events per hour in a particular plot over the year period (Zavaleta *et al*., 2014) was collected, then compared between hotspots vs non-hotspots using one-way ANOVA. Camera traps images were grouped into months based on stamped date on images, then separated into dry and wet season, thereafter compared between images captured during dry vs images captures between wet season for both hotspot and non-hotspot areas over the year period using one-way ANOVA termite mounds and grazing lawns separately. Camera traps images were separated into those captured during the day vs night, grouped into different ungulates thereafter converted into percentages to know the extent of diurnal vs nocturnal if any descriptively.

In hotspots attractiveness experiments, *Cynodon dactylon* grass growth height was measured for 61 days in various pots containing soil derived from termite mounds, grazing lawns and control, averaged, thereafter compared using one-way ANOVA. Furthermore, grass N and P contents from pots containing soil from termite mounds, grazing lawns and control plots were averaged, tested for normality and compared using one-way ANOVA. Grass greenness was

assessed in each pot, scores from termite mound soil pots, grazing lawns pots as well as control plots were averaged and compared using one-way ANOVA. In fertilizing experiment, grass N and P contents before setting experiment, after application of fertilizer and controls were averaged in study plots, then compared for statistical difference using one-way ANOVA. Ungulate presence using tracks and dung depositions separately were averaged in fertilized plots, clipped plots vs control plots, tested for normality, thereafter one-way ANOVA was used to determine differences between means across experimental plots. Grass height and tufts usage estimates in fertilizing, clipped and their respective control plots, termite mounds, grazing lawns and their controls were averaged separately, thereafter, compared using one-way ANOVA. Grass tufts usage were estimated by placing a quadrat of 1 m^2, estimating visually in percentage the extent to which grass was eaten, eaten tufts were identified as grass that had been eaten partially or fully by the animal and leaves were cut. Ungulate presence (dung and tracks) were compared between dry and wet season by separating the data for dry and wet season months, thereafter compare them using one-way ANOVA.

Isotopic signatures from grass sprayed with urea close to the termite mounds were compared with control grass from non-termite mounds (controls) using one-way ANOVA. Grass sprayed with urea from termite mounds were also compared with dung isotopic signatures deposited within 30 m from the sprayed grass using one-way ANOVA to evaluate isotopic signature similarity and differences (Miranda *et al*., 2014). Tukey's Post-hoc test was used in all statistical tests, significant levels were set at $\alpha = 0.05$. Software used was Origin Pro 8 (Serrano *et al*., 2011).

CHAPTER FOUR

RESULTS AND DISCUSION

4.1 Results

4.1.1 Grass and soil nutrient characteristics on hotspots and controls

In average, circumference of mounds was 20 m, while average height was 1.5 m. A total of 17 grass species were found across the study plots, of which *Hyparrhenia hirta, Andropogon gayanus, Digitaria* spp, *Themeda triandra, Panicum repens* and *Oryza longistaminata* were most frequently encountered. Grass species richness differed slightly between termite mounds and controls but not between grazing lawn and control plots (Tables 1 and 2), while grass species diversity did not differ (Tables 1 and 2).

Table 1: Summary of variables assessed for grass and soil samples on termite mound sites vs control sites with their respective sample size (N), *F* value, *P* value, *t* value and degree of freedom (df) values

Variable	Termite mound	Control	N	*F*	*P*	df
Grass species richness	13±7	14±3	45	3.34	0.027	(3,44)
Diversity index (Shannon)	2.14	2.08	40	t = 0.29	0.773	(37.2)
Height (cm)	55±5	39±3	40	55.42	<0.0001	(3,36)
Dry biomass (g/m^2)	238±42	172±25	40	2.20	0.104	(3,36)
Grass greenness score	3.6±0.3	2.5±0.3	10	t= 12.07	<0.0001	(9)
Basal cover (%)	24±11	18±8	26	0.67	0.644	(5, 25)
Grass N (%)	0.26±0.04	0.13±0.02	17	25.55	<0.0001	(3, 16)
Soil N (%)	0.21±0.04	0.09±0.04	13	13.57	0.0004	(3,12)
Grass P (mg/kg)	238±82	113±36	17	13.29	0.0001	(3,16)
Soil P (mg/kg)	236±62	107±13	13	7.96	0.0034	(3,12)

Table 2: Summary of variables assessed on grazing lawn sites vs control sites with their respective sample size (N), *F* value, t value, *P* value and degree of freedom (df) values

Variable	Grazing lawn	Control	N	F	P	df
Grass species richness	11±3	11±3	57	0.053	0.983	(3,56)
Diversity Index (Shannon)	1.808	1.746	73	t = 0.32	0.751	(71.8)
Height (cm)	47±3	60±3	21	17.46	<0.0001	(3,20)
Dry biomass (g/m^2)	214±38	278±43	21	0.77	0.524	(3,20)
Grass greeness score	2.5±0.58	1.8±0.4	6	t =2.12	0.086	(5)
Basal cover (%)	20±31	20±21	25	0.26	0.932	(5,24)
Grass N (%)	0.30±0.040	0.15±0.03	17	18.42	<0.0001	(3,16)
Soil N (%)	0.81±0.01	0.23±0.03	8	13.67	0.014	(3,4)
Grass P (mg/kg)	424±178	222±59	20	4.68	0.015	(3,16)
Soil P (mg/kg)	543±106	211±18	5	8.14	0.035	(3,4)

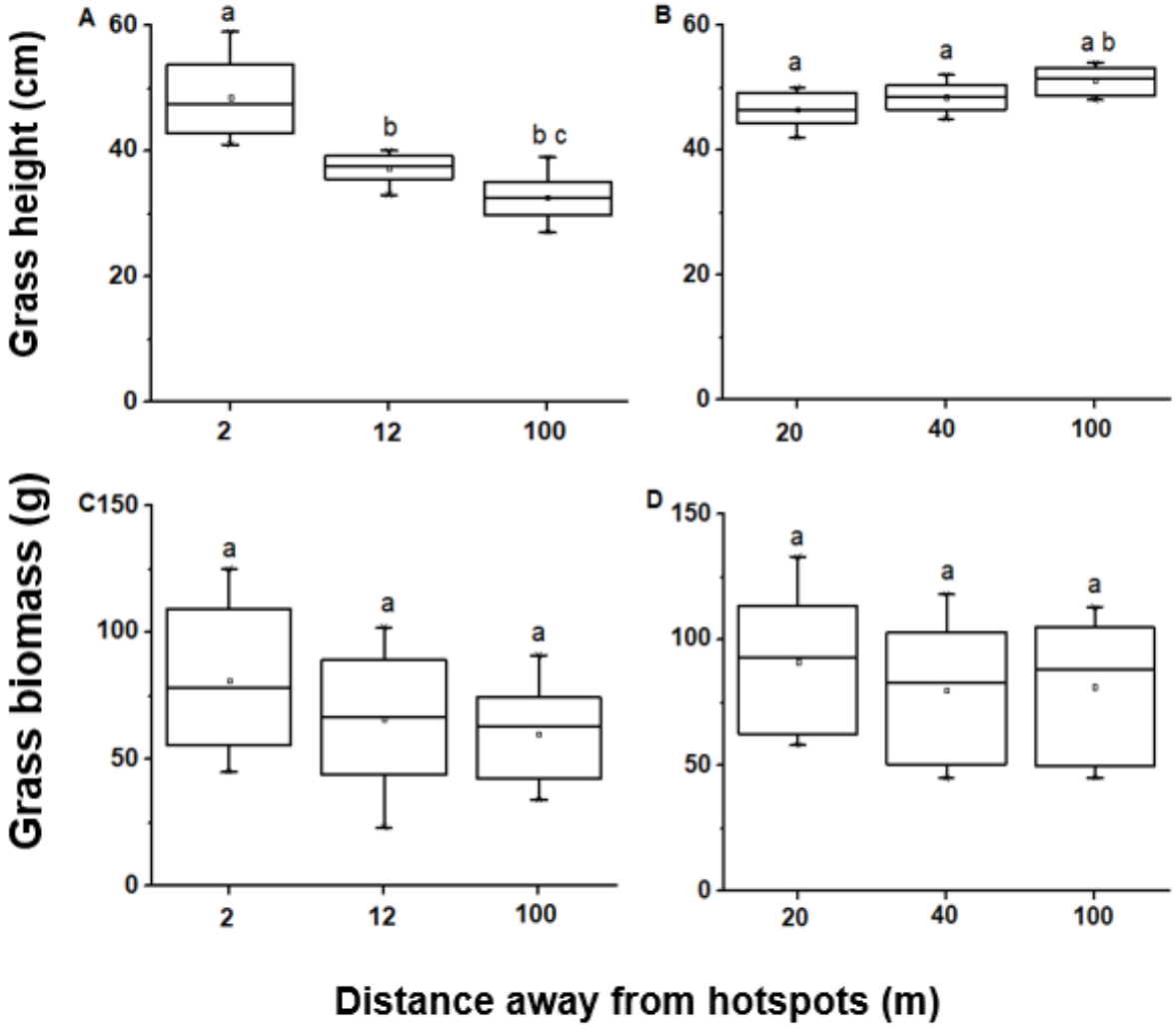

Figure 3: Mean grass height (in cm) and grass biomass (in g) measured as moving away from the influence of termite mounds (A, C) and grazing lawns (B, D), respectively

Grasses from termite mounds were on average almost twice as tall as control grasses and 7% shorter in grazing lawns vs control sites (Tables 1 and 2). With increasing distance away from termite mounds ($F_{2, 27}$ = 36.39, P < 0.0001), grass height decreased while grass height increased further away from grazing lawns ($F_{2, 15}$ = 5.04, P = 0.021; Fig. 2). Grass biomass did not significantly differ between termite mounds, grazing lawns and their control areas (Tables 1 and 2) nor did it change when moving away from termite mounds and grazing lawns ($F_{2, 27}$ = 1.85, P = 0.176 and $F_{2, 15}$ = 0.301, P = 0.744 respectively; Fig. 2). Grasses were greener on termite mounds compared to their respective control sites (Table 1) but not in grazing lawns vs control sites (Table 2). Generalized Linear Mixed Model analysis show that site (hotspot vs control) and location (distance away from hotspot) are the largest

contributor to the variation in greenness level (with F_1 = 35 and P < 0.001 for site and F_1 = 119 and P < 0.001 for distance). Grass basal cover did not differ significantly between termite mound and control areas nor grazing lawns and controls (Tables 1, 2). Grass leaf N content of *H. hirta* was by 34% higher while soil N content was about two times higher on termite mounds compared to that in control areas (Table 1). Further, GLMM analysis show a strong interaction between nutrient hotspot location, distance and their interaction with nutrient content (N) (with F_1 = 41.95, P < 0.001 for hotspot location and F_1 = 20.11, P < 0.001 for distance). Grass leaf P content of *H. hirta* and soil P contents were more than twice as high as those in control areas (Table 1). *Hyparrhenia hirta* grass leaf N and P contents in grazing lawns were also about twice as high as those in control areas (Table 2). Furthermore, soil N and P contents were three times and twice as high, respectively, in grazing lawns compared to control sites (Table 2).

4.1.2 Ungulates grazing frequency in hotspots and controls

Grass tuft usage estimates decreased significantly with increasing distance from termite mounds ($F_{2,27}$ = 74.17, P < 0.0001; Fig. 4 a). Generally, grass tuft usage signs in termite mound areas were twice as high as those in control areas ($F_{2,18}$ = 123.07, P < 0.0001). When moving away from grazing lawns, grass tuft usage decreased ($F_{2,15}$ = 25.68, P < 0.0001; Fig. 4 b), whereby tuft usage estimates around grazing lawns were twice as high compared to controls ($F_{1,10}$ = 192.96, P < 0.0001). There was a strong interaction between grass tufts usage and location, distance, season against nutrient contents (N, P) P < 0.001. In this study, based on grass preference index analyses, the most frequently consumed species were *Hyparrhenia hirta* (scored 88%) and *Andropogon gayanus* (scored 64%), while *Sporobolus* spp was not preferred (scored 0%).

Dung and track frequency was seven and 15 times higher, respectively, in termite mound areas than in control areas ($F_{1, 22}$ = 10.66, P = 0.0035 and $F_{1, 22}$ = 8.83, P = 0.007; Fig. 4 c and d respectively). In addition, dung deposition and tracks were three times more frequent in grazing lawns compared to control areas ($F_{1, 22}$ = 16.33, P < 0.0001 and $F_{1, 22}$ = 23.74, P < 0.0001; Fig. 3 and 5 a, respectively). The three most frequently observed grazing ungulate species based on tracks and dung were hartebeest, roan antelope and reedbuck (Fig. 5 b). In termite mound areas, roan antelope was responsible for 78% of the visitation activity (mean tracks and dung deposition), hartebeest for 21%, while reedbuck only contributed 1% (Fig. 5

b). In grazing lawns, roan antelope was responsible for 30% of the visitation activity, while reedbuck and hartebeest contributed 25% and 44% respectively (Fig. 5 b).

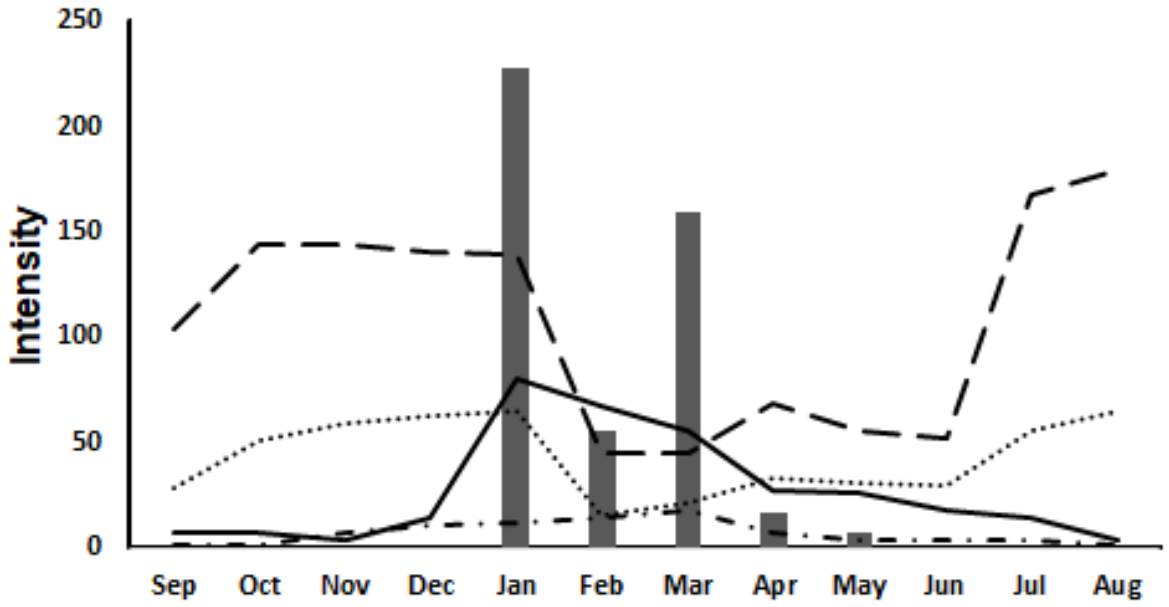

Figure 4: Rainfall amount in mm (columns) at the Issa valley and ungulate presence according to the frequency of dung depositions in grazing lawns (dashed), non-grazing lawns (dotted), termite mounds (solid) and non-termite mounds (dotted)

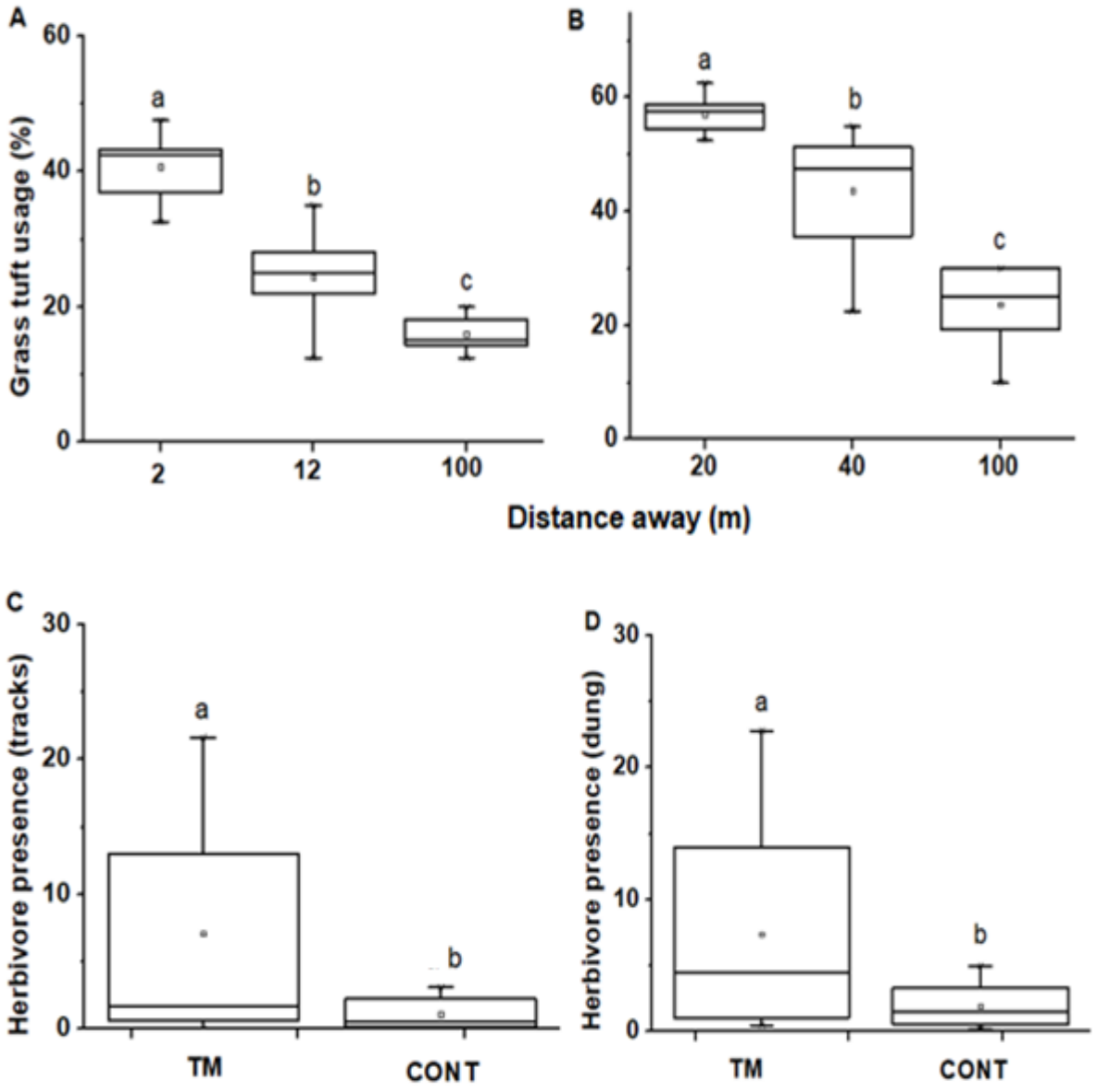

Figure 5: Grass tuft usage estimates in % when moving away from (A) termite mounds (TM) and (B) grazing lawns (GL). Ungulate presence averaged using tracks (C) and dung (D) between termite mounds (TM) vs control (CONT)

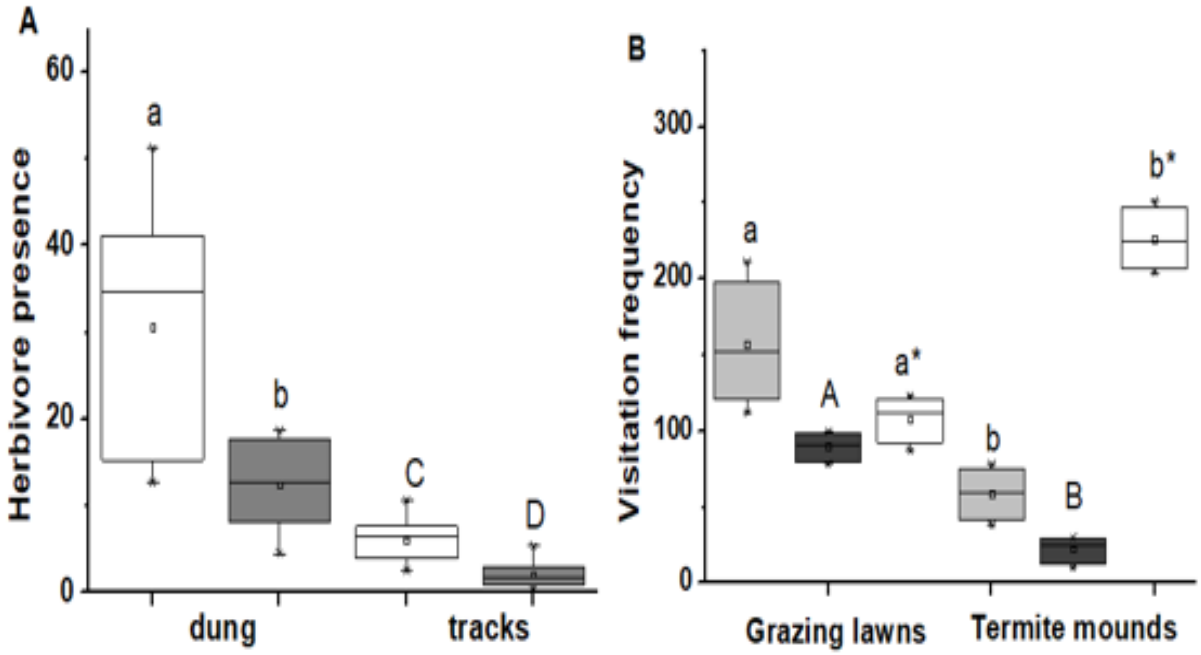

Figure 6: A. Herbivore presence using dung in grazing lawns (white vs controls (grey) and using tracks in grazing lawns (white) vs controls (grey). B. Herbivore visitation frequency, hartebeest (grey), reedbuck (black) and roan antelope (white) in GL and TM

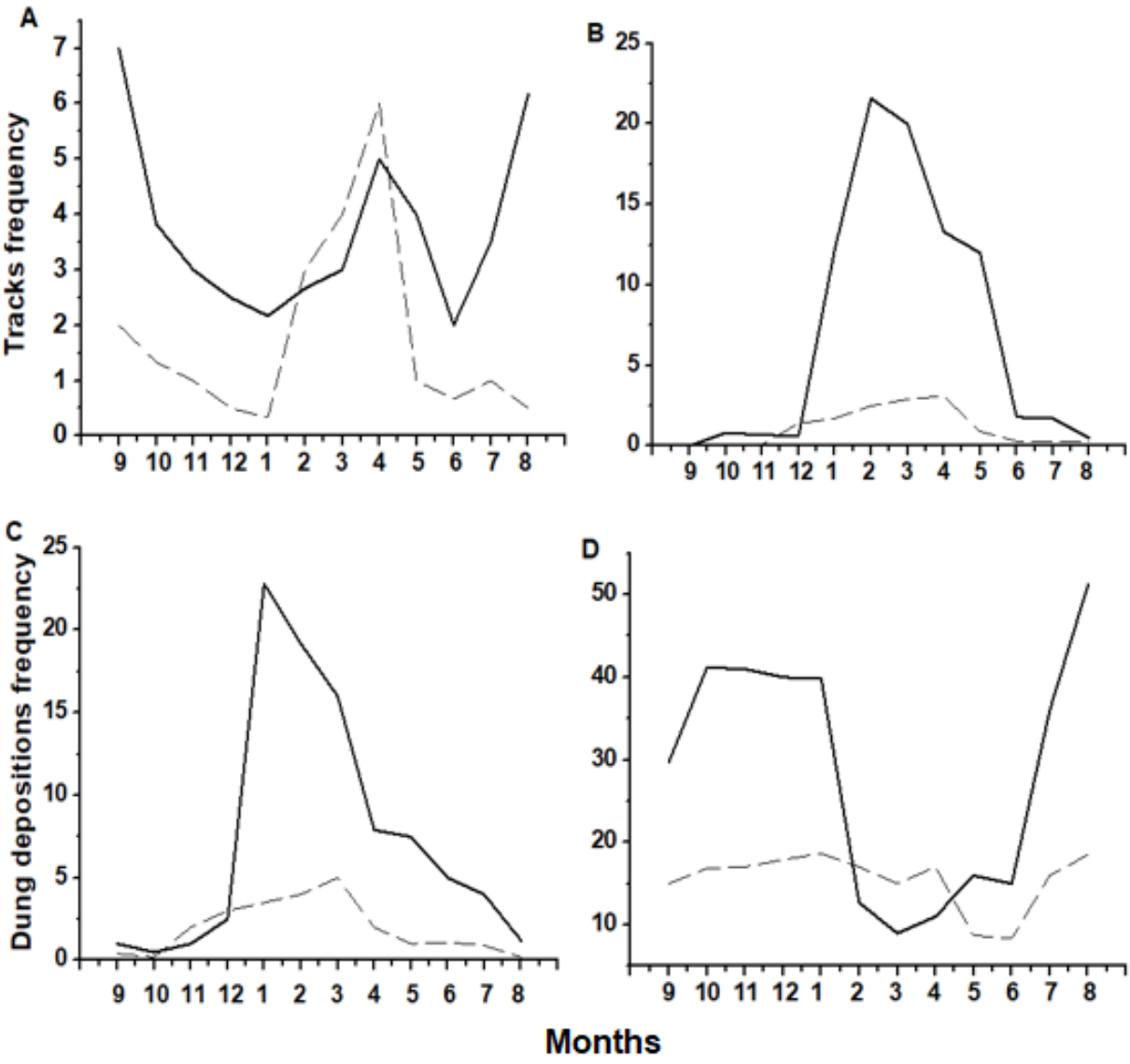

Figure 7: Herbivore presence using (A) tracks between GL (solid) vs CONT (dashed) (B) tracks between TM (solid) vs CONT (dashed) (C) dung depositions between TM (solid) vs CONT (dashed) and (D) dung in GL (solid) vs CONT (dashed) over year period

Dung deposition on termite mounds was four times as frequent during the wet season ($F_{1, 10}$ = 10.17, P = 0.009; Fig. 6 c), while tracks were eight times more frequently observed during the dry season ($F_{1, 10}$ = 16.36, P = 0.002 (Fig. 6 a). In grazing lawns, dung depositions were twice as frequent in the dry season than in the wet season ($F_{1, 10}$ = 7.13, P = 0.02; Fig. 6 d), while tracks show no seasonal difference ($F_{1, 10}$ = 7.51, P = 0.97; Fig. 6 c). Grass height differed significantly between seasons, with taller grasses on termite mounds during wet season vs shorter grasses during dry season ($F_{3, 36}$ = 55.4, P < 0.0001), whereas grass tuft usage was higher on termite mounds compared to control areas and grazing lawns compared

to control areas ($F_{5, 54}$ = 153, P < 0.0001) and ($F_{5, 30}$ = 64.5, P < 0.0001) respectively. Grass biomass was higher on termite mounds and grazing lawns in the wet season compared to the dry season ($F_{2, 27}$ = 47.3, P < 0.0001) and ($F_{2, 15}$ = 5.9, P = 0.012) respectively, with season being the largest contributor to the variation in grass biomass (F = 245.79, P < 0.001); plate 1.

Plate 1: Termite mound area during rainy season

Plate 2: Termite mound grass during dry season

4.1.3 Ungulates grazing frequency using camera traps footage around hotspots and controls

Ungulate presence using camera traps was four times higher in hotpots (both termite mounds and grazing lawns combined) vs control areas ($F_{1, 18}$ = 11.93, P = 0.0028; Fig. 7 a). Around termite mounds only, animals were captured four times more frequently than in control sites ($F_{1, 18}$ = 10.23, P = 0.004), and the same pattern was visible for grazing lawns ($F_{1, 18}$ = 6.05, P = 0.024; Fig. 7 b). Ungulate images captured during the wet season were thirty two times higher around termite mounds ($F_{1, 8}$ = 16.71, P = 0.003) and grazing lawns ($F_{1, 8}$ = 2.33, P = 0.16; Fig. 7 b) compared to the respective control sites. Ungulate images captured during dry season were not significantly different around termite mounds compared to controls ($F_{1,12}$ = 0.09, P = 0.76) and grazing lawns were six times higher than their controls ($F_{1,12}$ = 3.78, P = 0.07).

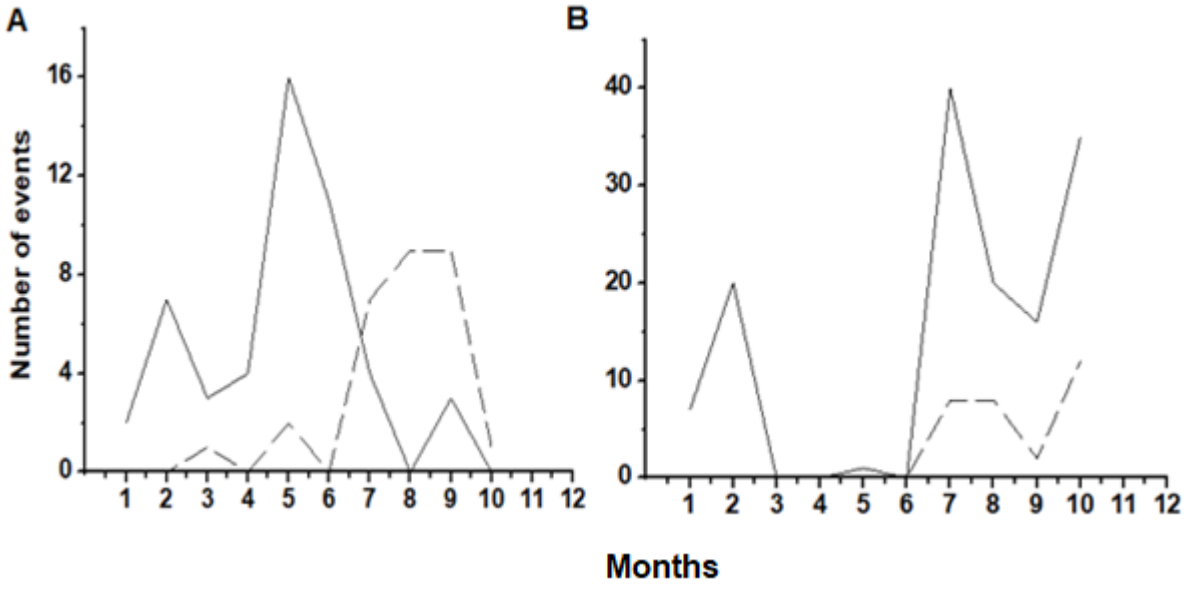

Figure 8: Animal visitation as number of event per hour captured by camera traps (A) around termite mounds (solid line) vs non termite mounds (dashed line) and (B) around grazing lawns (solid line) vs non grazing lawns (dashed line)

If the animal was photographed more than once by the same camera within 1 h, this was considered as one event. Animal visitation events did not differ significantly between night and day in hotspots ($F_{1, 30}$ = 0.42, P = 0.518).

Table 3: Animal species that were captured by camera traps in hotspot areas from May 2016–October 2017

Taxonomic group	Scientific name	Common name	Capture events	
			Dry season	Wet season
Primates	*Papio cynocephalus*	Yellow baboon	2	3
	Pan troglodytes schweinfurthii	Chimpanzee	1	0
Ungulates	*Potamochoerus porcus*	Bushpig	2	2
	Tragelaphus scriptus	Bushbuck	0	10
	Alcelaphus lichtensteinii	Hartebeest	49	10
	Oreotragus oreotragus	Klipspringer	1	11
	Redunca redunca	Reedbuck	129	32
	Hippotragus equinius	Roan antelope	32	16
Carnivora	*Mellivoria capensis*	Honey barger	1	1
	Panthera pardus	Leopard	0	1
	Crocuta crocuta	Spotted hyena	1	0
	Civettictis civetta	African Civet	5	0
	Genetta angolensis	Miombo genet	6	0
	Herpestes ichneumon	Mongoose	1	0
Rodents	*Hystrix africae-australis*	Porcupine	7	0

Plate 3: Termite mound grass burning during dry season

4.1.4 Factors for hotspots attractiveness

In the fertilizing and clipping experiment, grass leaf N and P values collected at the beginning of the experiment differed significantly from those collected at the end of the experiment and, as expected, between fertilized and control plots (For N: $F_{2, 16} = 118.78$, $P < 0.0001$, for P: $F_{2, 16} = 14.91$, $P < 0.0001$; Fig. 8 a, b). Upon using generalized linear mixed model (GLMM), Ungulate tracks and dung were about ten times as frequent in clipped and fertilized plots than in control plots ($F_{2, 18} = 13.11$, $P < 0.001$; Fig. 8 c and $F_{2, 18} = 8.44$, $P = 0.0025$; Fig. 8 d). Grasses were on average by about 5 cm higher in fertilized vs control plots ($F_{2, 258} = 412.46$, $P < 0.0001$; Fig. 9 a). Furthermore, grass tuft was highly eaten in fertilized plots and clipped plots compared to control plots ($F_{2, 269} = 96.42$, $P < 0.0001$; Fig. 9 b).

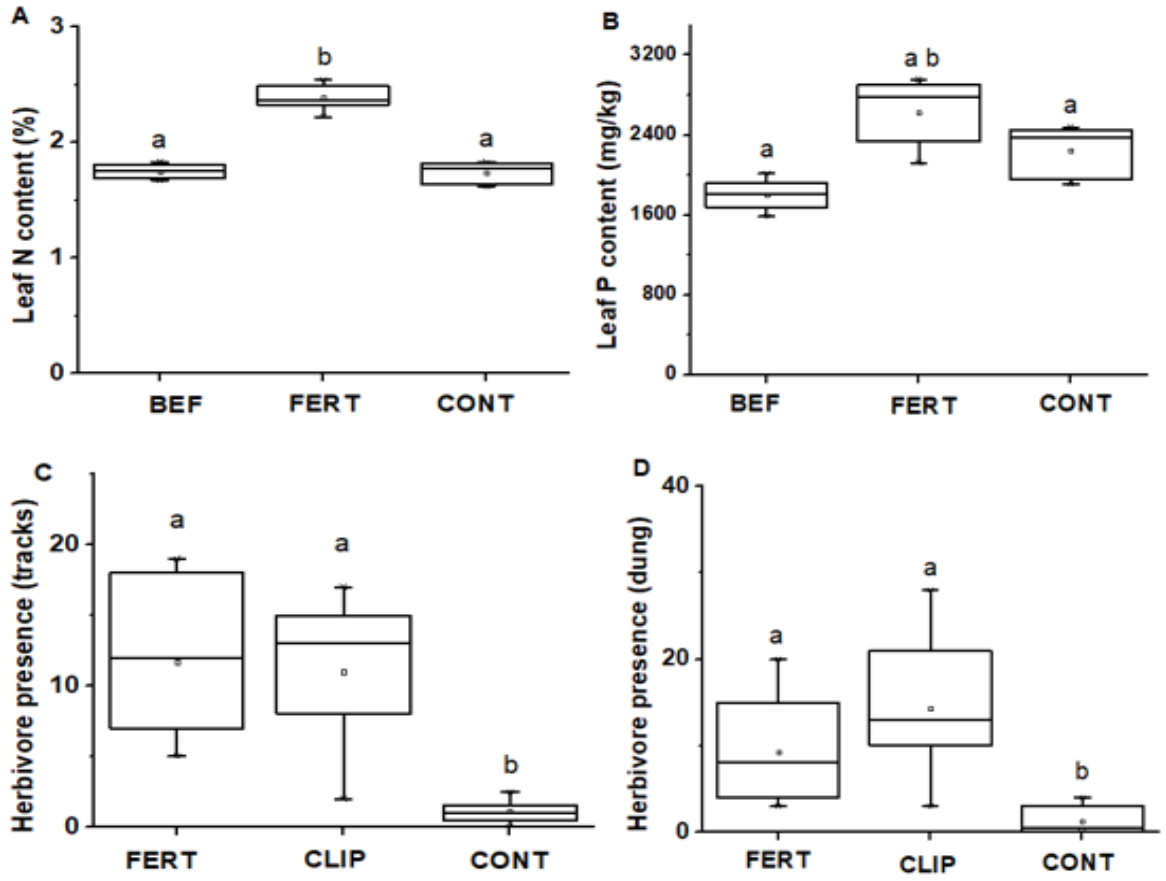

Figure 9: Grass leaf N contents (A) and P contents (B) before setting experimental plots (BEF), in fertilized (FERT) vs control (CONT) plots. Herbivore presence using tracks (C) and dung (D) in fertilized (FERT), clipped (CLIP) and control plots (CONT)

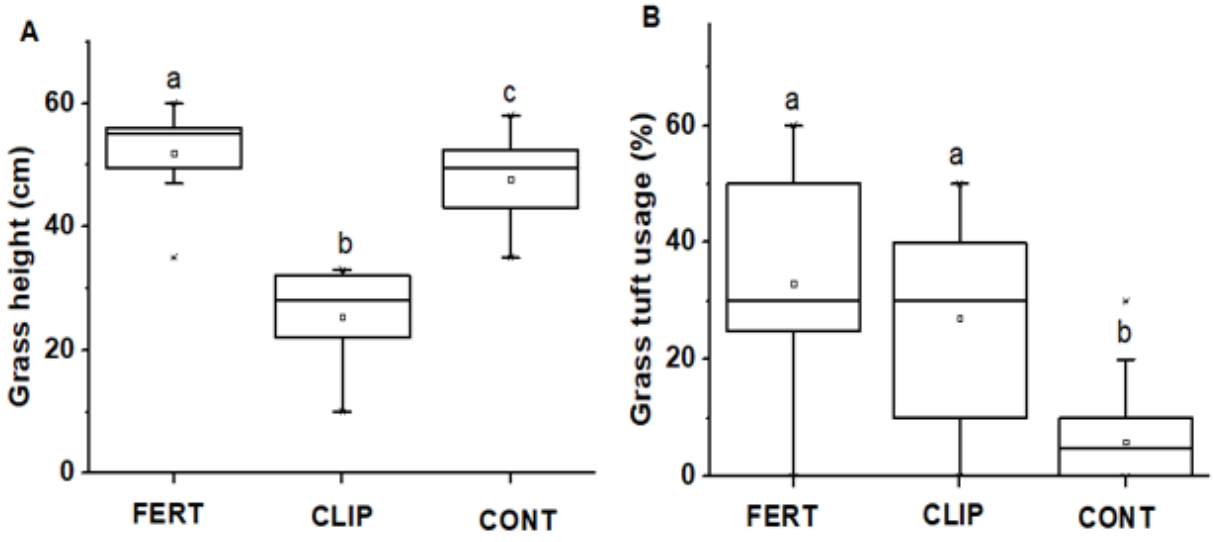

Figure 10: Average (A) grass height and (B) tuft usage between fertilized (FERT), clipped (CLIP) and control plots (CONT)

In pot experiment, study found that *Cynodon dactylon* height differed significantly across pots with termite mound soil, grazing lawn soil and control area soil ($F_{2,180}$ = 61.57, P < 0.0001, Fig. 10 a). Grasses in termite mound soil was 34% greener than control site pots while grasses grown in grazing lawn pots was 24% greener than control sites ($F_{2,\ 180}$ = 296.69, P < 0.0001) Fig. 10 b). Grass leaf N and P contents of *C. dactylon* in pots with termite mound soils were three times and twice as high as those from control plots ($F_{2,\ 19}$ = 73.24, P < 0.0001 and $F_{2,\ 19}$ = 18.25, P < 0.0001, respectively; Fig. 10 c, d).

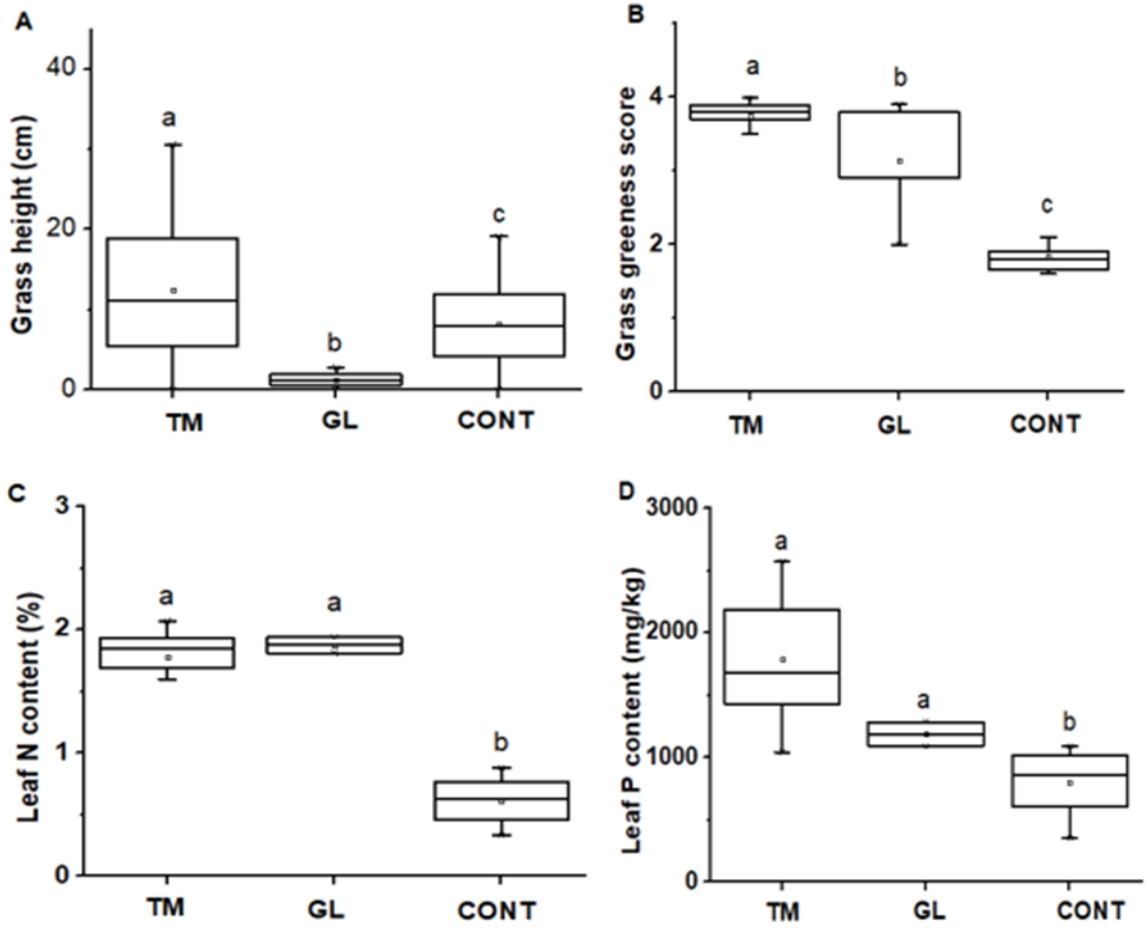

Figure 11: Mean of (A) average Cynodon dactylon grass growth height, (B) average greenness score, Nitrogen (C) and Phosphorus (D) contents in pots containing soils from TM, GL and CONT

4.1.5 Wide reaching nutrients re-distribution

There was a statistical significance difference in $\delta^{15}N$ between urea sprayed grass, control grass and dung deposited within a 30 m radius around the termite mounds ($F_{2,\ 45}$ = 40.23, P < 0.0001). Tukey's post hoc analysis show no difference between urea sprayed grass and dung

(fig. 11). Urea sprayed grass around termite mounds had about twice as high values in $\delta^{15}N$ compared to unsprayed grass in controls ($F_{1, 28}$ = 39.07, P < 0.0001, fig. 12). Further, there was a positive correlation between $\delta^{15}N$ of dung deposited close to the mounds than far away from mounds ($F_{1, 30}$ = 3.84, R^2 = 0.347, P = 0.059; Fig. 12).

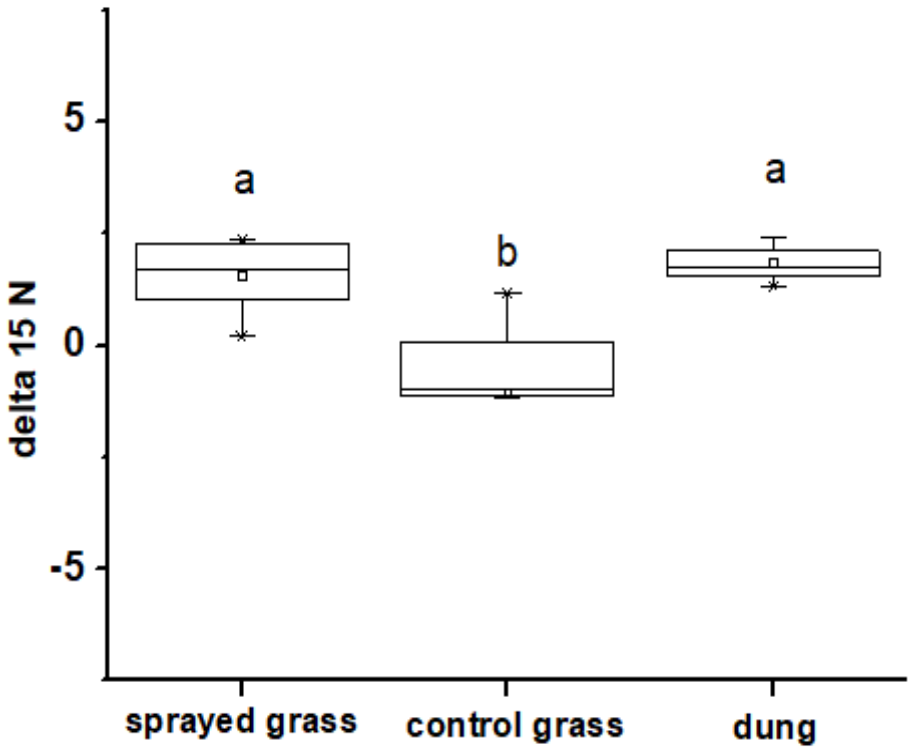

Figure 12: Isotopic δ15N plot of urea sprayed grass (termite mound grass) vs unsprayed grass in controls and vs roan antelope dung deposited within a 30 m radius from urea sprayed termite mounds

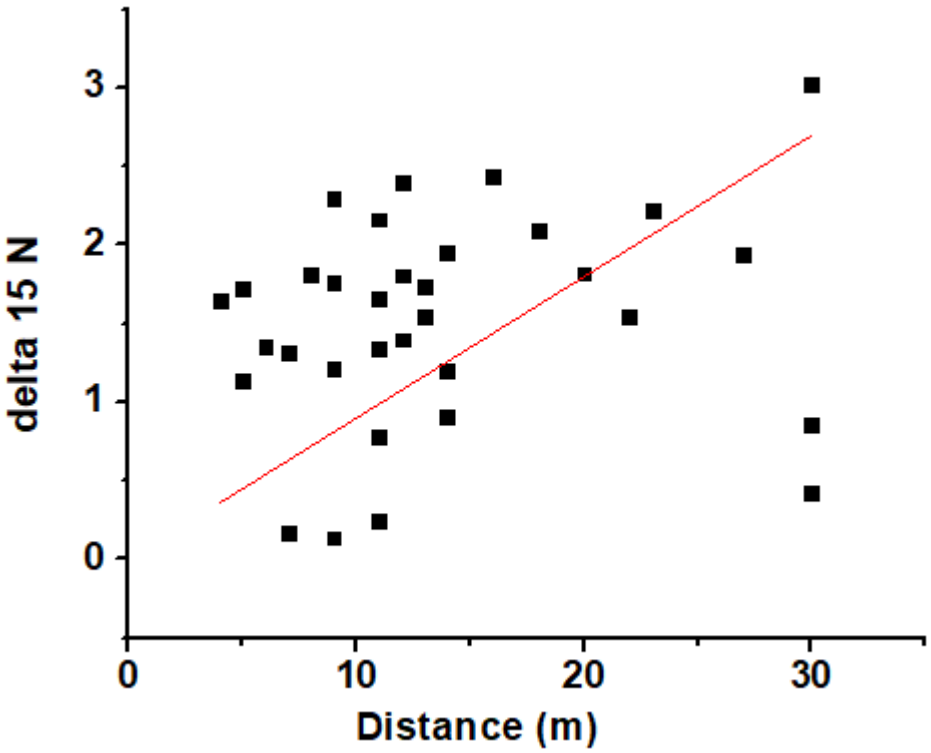

Figure 13: Isotopic δ15N in dung deposited with 30 m radius from urea sprayed termite mounds vs the distance of dung deposition away from the termite mound centre

4.2 Discussion

4.2.1 Grass and soil characteristics on hotspots

This study highlights that nutrient hotspot areas offer important feeding grounds for various grazers in western Tanzania, in accordance with previous studies (Grant & Scholes, 2006; Treydte *et al*., 2007). Grass height around termite mounds was taller than height from control sites, which is similar to studies in South Africa (Moe *et al*., 2009; Steinke & Nel, 1989). Further, study found no differences in grass biomass between grazing lawns and controls in contrast to (Davies *et al*., 2016) and (McNaughton, 1984b) who found that grazing lawn areas show reduced grass biomass due to high utilization by grazers. In this study, grazer presence was generally low and grazers were rarely seen on grazing lawns, hence they might not have had a great reduction effect on the lawn grass biomass overall (Austrheim *et al*., 2014; Holdo *et al*., 2013) and grazing lawns might have been created in times when grazers had been more present in that area (Ogawa *et al*., 2012). Grass species richness around termite mounds differed from control sites, but not for grazing lawns and their control sites, and the most dominant grass species at all sites was *Hyparrhenia hirta*. This is similar to Davies *et al*.

(2014), Moe (2005) and Muvengwi *et al*. (2017) who also found differences in species richness between termite mounds vs controls. *Hyparrhenia hirta* was preferred by grazers, which was also reported for grazing ungulates in South Africa, particularly by roan antelope and hartebeest (Taolo, 1995; Roosendaal, 1973). Understanding preferred grass species and locations is important for management as grazers will disperse into preferred hotspots in which their distribution can then be predicted (Archibald, 2008).

4.2.2 Ungulates' grazing frequency by indirect methods around hotspots and controls

This study found spatially concentrated dung depositions, which are highly important for nutrient input in soils and elevate grass nutrients, in close proximity to nutrient hotspots, which will further promote grass quality (Coetsee *et al*., 2011; Cromsigt & Kuijper, 2011; Roberts, 2009). In addition to nutrient input, grazing stimulated fresh regrowth, which occurred on termite mounds during the wet season, further attracting ungulates. This is in contrast to (Tyrrell *et al*., 2017), who reported that during the wet season time, grazers spread out for foraging because fresh grass is widely distributed. In the dry season, grazers are under pressure due to nutritionally-deprived forage (Davies *et al*., 2016), which is when they visited grazing lawns more often in this study. Despite the lack of green grass in the dry season at Issa, termite mounds were still used as climbing stones for grazers, likely for scanning the landscape for predators. Further, study results show that grass tufts were found to strongly interact with distance, season and nutrient availability. However, grazing impact is measured subjectively and only into categories but this study refers to other studies that have recorded grazing impact (Treydte *et al*., 2010, 2011; Treydte *et al*., 2013).

This study is aware that hotspot size can affect species diversity (Cook *et al*., 2014), and results here provide only a snapshot of grazer activity, grass and soil properties as well as nutrient cycling. Grazing lawns sample size in this study were about 1 ha in size (70 x 70 m), while the termite mound influence areas (sample size) were about 30 x 30 m. However, this study show that termite mounds, despite being small in size, still can act as small grazing lawns that grazers preferrably feed on, hence, increasing nutrient cycling through their dung depositions (Cromsigt & Olff, 2008). Further, these results were confirmed by camera trap data, revealing that ungulates frequently used hotspot sites. Hence, combination of various data assessment methods proved to be an effective and efficient way in understanding how wild ungulates use hotspot areas.

Plate 4: Dung deposited by hartebeest

Plate 5: Track of roan antelope

4.2.3 Ungulates grazing frequency by camera traps footage in hotspots and controls

This study also found that roan antelope and hartebeest deposited more dung around hotspots than reedbuck did, which might be due to their relative numbers within study area, which was confirmed by camera trap events. However, data on the population estimates of different ungulate species in Issa valley are missing (Piel *et al*., 2018). Since roan antelope and hartebeest are larger in size than reedbuck, they might need a higher amount of good quality food from nutrient rich areas (Shipley, 1999) and they were found to frequently return to previously visited areas (Morales *et al*., 2005). Large ungulate grazing is affected by abiotic factors such as slope and distance to water (Senft *et al*., 1996) as well as biotic factors such as forage quality and quantity (Bowyer *et al*., 1998; Senft *et al*., 1996; Treydte *et al*., 2006). However, for large ungulates such as roan antelope and hartebeest, foraging velocity decreases and intake rate increases once they reach areas of abundant palatable grass (Senft *et al*., 1996) which was confirmed by this study results. This study, used a combination of animal presence estimates using dung depositions (Treydte *et al*., 2010) and camera traps

(Rendall *et al*., 2014). The use of camera traps in ecological studies has increased (Wearn & Glover-Kapfer, 2017) and is an effective measure for monitoring wild animals in a non-invasive way (Ancrenaz *et al*., 2012; Kays *et al*., 2009, Rendall *et al*., 2014). Camera trap footage show higher animal activity around grazing lawns during the dry season than during the wet season and higher animal activity during rain season compared to dry season around termite mounds, this could probably happen because of the impact of foraging resources (Anderson *et al*., 2010) around hotspots in different seasons. Camera trap images show that reedbuck (plate 7) and hartebeest (plate 6) were frequently visiting the grazing lawns, which might be due to high nutrient availability in these areas (Cromsigt & Olff, 2008) or the lower susceptibility to predation (Anderson *et al*., 2010). Reedbuck strongly prefer flat, low lying land (Kingdon & Hoffmann, 2013) which was represented by grazing lawns in the Issa valley. Similary, hartebeest prefer short grasses (Schuette *et al*., 2006) in low lying areas, which were also found on grazing lawns in this study.

Plate 6: Group of hartebeest and roan antelope grazing around grazing lawns

Plate 7: Group of reedbuck grazing around grazing lawns during the night

4.2.4 Hotspots attractiveness experiment

This study found that grazers strongly exploited fertilized plots, a result that is consistent with earlier findings in South Africa (Cromsigt & Olff, 2008). In addition to nutrients, study also found that clipped plots, i.e., with a favorable grass structure and fresh regrowth, were strongly used by ungulates. As grazing lawns are open areas with short and nutrient-rich grasses defined by frequent grazing (Hempson *et al*., 2015), they easily attract animals, particularly grazers. However, very few experiments have sought to assess the structural and physiological factors that draw animals to resources (Cromsigt & Olff, 2008). Here, study identified the factors that might make nutrient hotspots attractive and show that grass appearances as well as nutrients are important factors for grazers. Additionally, camera trap pictures revealed that spotted hyena *(Crocuta crocuta)* and leopard (*Panthera pardus*) are among the most frequent predators in the study area, often found on grazing lawns, which might have influenced ungulate distribution and resource use in study area (Radloff & Toit,

2004). In addition, the results of experiment may have been affected by local people harvesting *Orchid* species in June 2017 close to study sites. Furthermore, a total of 40 plots were affected by wild fires between July and August 2017. This jeopardized longer-term observation on grazing lawn attractiveness. This study is aware that results here provide only a snapshot of ungulate-ecology interactions in the ecosystem. Results show that grazing lawns were frequently visited, particularly in the dry season, which might be due to their openness (Hempson *et al*., 2015). However, termite mounds, despite their small size may also act as small grazing lawns as grazers intensely feeding on their vegetation may increase the nutrient input through their dung over time (Cromsigt & Olff, 2008), which in turn might again affect forage selection by grazers (Howery *et al*., 2010). Furthermore, hydrological properties of termite mounds (Chen *et al*., 2019; Jamilu & Biswajeet, 2018) in combination with their nutrient properties may further contribute to their important role as hotspots. In the African savanna, termite mounds are conspicuous long lived structures (Levick *et al*., 2010), whether active or inactive may be occupied by fungus growing Macrotermes, further inactive mounds are liable to be recolonized and to become active again at any time (Acanakwo *et al*., 2019) hence remain nutrient rich areas.

Onsite experimental plot used in this study show that fertilization enhanced grass greenness and, thus, might have made the grass more attractive for grazers, as indirect observations suggest. Additionally, termite mound areas had high soil N and P levels, impacting the nutrient levels of grass as well as appearance of the grass. Furthermore, distance away from hotspots strongly impacted grass and soil nutrient contents. Fertilized plots show the highest frequency of grazer visits compared to their respective control sites, which suggests that raising nutrient input may attract ungulates (Cromsigt & Olff, 2008; Hartley & Mitchell, 2005). Hence, this study findings confirm observations on the selectivity of ungulates in miombo systems, and show which clues ungulates might use to find appropriate forage (Burkepile *et al*., 2013; Durant, Fritz & Duncan, 2004).

In pot experiment used in this study, pots with termite mound soil had the tallest and greenest *Cynodon dactylon* individuals compared to other soils, which clearly supports findings of previous work showing that termite mounds are nutrient sinks (Grant & Scholes, 2006; López-Hernández, 2001) and can strongly enhance grass nutrients and appearance (Taolo, 1995). *Cynodon* spp. grass is frequently found in Tanzania and widely used by wild and domestic grazers in eastern Africa (Mandal *et al*., 2017; Rita *et al*., 2012). Grass greenness,

reflecting high nutrient levels (Treydte *et al*., 2010), might be an important cue for ungulates (Bhola *et al*., 2012; Burkepile *et al*., 2013). Hence, this study results show that termite mound soils favors growth of quality grass which are highly important attractants for grazers. Pots with grazing lawn derived soils did not store water effectively, which was likely due to the soil type, hence *C. dactylon* grass did not grow better, despite the high nutrient content of these soils. Moisture stress and elevated temperature can suppress the growth of *C. dactylon* (Mandal *et al*., 2017), thus rendering observed grazing lawns unlikely to serve as a nutrient hotspot in the miombo ecosystem.

4.2.5 Wide reaching nutrients re-distribution

Stable isotope technique, a method rarely used for terrestrial ecological studies in eastern Africa, highlighted spatial distribution of foraging and defecating of wild animals with respect to plant nutrient distribution. Isotope Ratio Mass Spectrometry (IRMS) is a novel approach used to provide useful information on the chemical and biological origin of various components (Muccio & Jackson, 2009; Reitsema, 2015). Measurement of isotope ratios can effectively be used to differentiate samples, which otherwise share similar chemical signatures (Muccio & Jackson, 2009). However, uncertainity may occur over the relative contribution of diet and water to tissue (Jardine *et al*., 2017) which might cause isotopic differences locally and temporally. Hence, a strong initial spatial difference in isotopic composition is of high advantage as it shows the differences between ungulate species and their respective diet (Hobson, 1999). This fact made this study to use urea spray in order to clearly show the link between grazer and their forage.

Results show that urea sprayed termite mound grass was similar to dung deposited within a 30 m radius around termite mounds, which confirmed that dung deposited around termite mounds originated from grasses near termite mounds. Study propose that grazers enrich nutrient hotspot areas even further by depositing more nutrients via dung after foraging on these hotspot sites, similar to what Treydte *et al* (2006) found on former boma areas within a coastal savanna habitat. Since this study did not use an adhesive after spraying urea and because study was conducted during the rainy season, urea signatures might have been affected and effects weakened due to rain events (Carlo *et al*., 2009). In addition to that, physiological and metabolic processes within ungulates after eating grass might also have affected results, diluting potentially strong differences (Zanden *et al*., 2014). However, this study results still show strong isotopic differences between sprayed urea grass and unsprayed

urea and strong similarities beween dung and hotspot grass. Hence, this study, in combination of other supporting data like dung deposition, tracks, tufts usage (Mayengo *et al*., 2020) and isotopic data provides enough strength for the results, hence acting as an important cue in highlighting spatially determined foraging resources and nutrient deposition.

Understanding how nutrients are transferred from high nutrient areas to low nutrient areas is an important aspect in ecology (Holtgrieve *et al*., 2009). An impressive example in is the large influx of nutrients as shown by dung depositions and stable isotope results in hotspot areas and the role played by grazers in transferring these nutrients from hotspot areas to nearby places (Treydte *et al*., 2006). Dung depositions can be used as proxy for describing habitat use of feeding mammalian wildlife (Treydte *et al*., 2006) and if grazers concentrate their dung depositions in hotspot areas, they promote nutrient cycling and generally impact forage quality around the hotspots, hence mantain the higher fertility in these areas (Mcnaughton & Banyikwa, 1997; Treydte *et al*., 2006).

CHAPTER FIVE

CONCLUSSION AND RECOMMENDATIONS

5.1 Conclusion

This study concludes that in miombo systems termite mounds and grazing lawns patches are important in maintaining grass quality for various grazers and that their importance differs across seasons. Furthermore, grazing lawns can be created through clipping and/or fertilization, which could be a restoration method especially in fragmented and uniform areas with a high risk of habitat degradation to stimulate ungulate-sustained grazing systems. Grass quality and structure are attractive factors for grazers, especially in an otherwise nutrient poor area like miombo ecosystem.

Combination of approaches used in data collection revealed to be effective in understanding ecological processes. Using camera traps, ungulates were found to spend more time grazing on hotspots than on control sites. Ungulate presence using dung depositions shows the same trend. Some species preferably graze at nutrients hotspots more compared to control sites. Furthermore, dung signature was more closely related to termite mound grass signature than to non-termite mound grass signature, hence, importantly, ungulates (grazers) are responsible for depositing nutrients in nutrient richer areas, enriching more these important feeding grounds, contribute into long persistence of these important areas in miombo ecosystems.

5.2 Recommendations

(i) Further work is needed for understanding how different termite species might impact grass growth, which attracts ungulates, as some mounds do not have grass growing on their soils at all. Also, identifying uses of termite mounds by local people and possible threats in different land uses should be explored.

(ii) More studies should be done on whether other nutrients, apart from N and P, impact grazing selectivity by different ungulates in miombo and savanna ecosystems.

(iii) Further studies should be done to identify whether there is competition in hotspot usage between ungulate groups of different body sizes.

(iv) Based on results obtained, study recommends more isotopic studies in combination with DNA metabarcoding, both in miombo and savanna systems, to precisely identify grass species preferred by various ungulates for improving their management options.

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